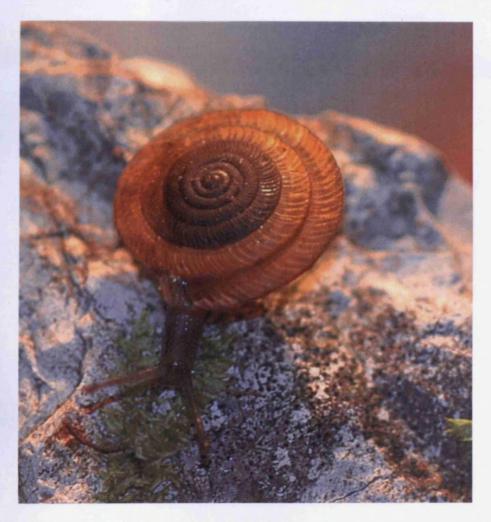
Pattern and process in southern Iberian land mollusc diversity

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SUMMARY

Locations in southern Iberia were sampled to assess patterns in the distributions and diversities of land molluscs and to determine the effects of habitat structure on diversity at differing scales.

In Part One of the study 91 sites, each 1km², were sampled. Species with higher abundances were present at more sites than those with lower abundances. Low levels of similarity were found between the land mollusc communities. The monthly mean of sunshine hours per day during the wet period and the annual mean absolute humidity provided the best explanation of the species data. The results suggest that the heterogeneous habitats from the region allow a large number of mollusc species to co-exist in varied communities possibly controlled by historical and regional factors including climate and geology.

In Part Two of the study 60 sites, each 1600m², were sampled. Twenty sites were located in each of three habitat types (sand, steppe and garigue), and for each habitat type ten sites were sampled in both the wet period and dry period. Diversities and habitat structure were assessed at 1m², 5m² and 20m². There were differences in the number of species, abundances and diversities between habitats, and between the wet and dry periods at each habitat. Increasing heterogeneity and complexity increased the number of species, but not their abundances. Components of habitat structure affected the number of species and abundances independently of the total complexity.

Relationships between heterogeneity, complexity, number of species and species diversity were scale-dependent with most of the statistically significant relationships between these occurring at 1m². Increases in abundances and number of species with increasing area support the passive sampling model and the area *per se* hypothesis.

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'Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?'

Charles Darwin, 1859

'We need, if possible, to look at the world from the molluscs' point of view, and it is unlikely that their categories correspond with our own.'

Arthur Edwin Boycott, 1934

'A key issue in ecology is how patterns of species diversity differ as a function of scale.'

Scheiner et al., 2000

CHAPTER 1. GENERAL INTRODUCTION

1.1 Introduction

The Mollusca is a monophyletic lineage that dates from the Lower Cambrian (Runnegar and Pojeta, 1985; Bruggen, 1995; Barker, 2001) and after the Arthropoda is the most diverse of all phyla (Morton, 1967; Rusell-Hunter, 1983). The general consensus is that there are seven extant classes: Aplacophora, Bivalvia, Cephalopoda, Gastropoda, Monoplacophora, Polyplacophora and Scaphopoda (Medina and Collins, 2003).

Estimates of the total number of mollusc species vary widely. Seed (1983) estimated about 100,000 species; Bruggen (1995) estimated between 40,000 and 200,000 species. Solem (1978) estimated the total number of land mollusc species to be about 24,000 but later (Solem, 1984b) stated that 30,000 to 35,000 should be thought of as a minimal estimate. Recent estimates by Lydeard *et al.* (2004) are similar to those of Solem (1978, 1984b) with 24,000 species of land molluscs, and between 11,000 to 40,000 undescribed species, while Cameron *et al.* (2005b) stated that there are at least 35,000 species.

Molluscs live in many habitat types but only the Gastropoda are found on land (Cain, 1983; Solem, 1984b). Land snails are not a monophyletic group and at least seven gastropod groups made the transition from aquatic to

terrestrial environments (Naggs and Raheem, 2005). Gastropods have a long and extensive fossil record, and their abundance and diversity in the Recent fauna has meant they have been used in many studies in various biological disciplines including evolution, ecology and biogeography (Riddle, 1983; Davison, 2002; McArthur and Harasewych, 2003).

1.2. Factors determining the distributions and diversities of land molluscs

The distribution of any species is limited by environmental factors (Hutchinson, 1965; Russell and Clout, 2004), and large-scale patterns of species diversities are determined by factors such as origination and extinction (Pearson and Carroll, 1999). Factors that determine the distributions and diversities of land molluscs include climate, temperature, geology, altitude, palaeoecological history and soil type (Valovirta, 1968; Bruggen, 1969, 1995; Cameron and Redfern, 1976; Peake, 1978; Jungbluth, 1979; Tattersfield, 1990; Kerney, 1999; Welter-Schultes, 2000; Carne-Cavagnaro et al., 2006), as well as colonization and habitat availability (Cameron et al., 2007).

Some of the factors determining distributions and diversities of land molluscs were considered by Solem (1984b; see also papers in Cameron *et al.* 2005a) in his world model of land snail diversity and abundance, where he stated that there is exceptional high diversity in the mid-North Island of New Zealand and gave the following as important factors for this diversity:

- stable and moderate moisture supply,
- very deep litter composed of items that curl,
- topography sheltered from desiccating winds,
- lack of disturbance for millions of years,

- small scale vegetation changes (Pleistocene and Holocene climatic fluctuations would have repeatedly separated then united forest patches; this may have allowed allopatric differentiation then subsequent coexistence after character displacement),
- minor predation pressure, and
- extended range

Chiba (2007) showed that moisture and productivity were important factors determining the number of species in the West Pacific Ogasawara Islands. Tattersfield (1996) reported that many of the species found in Kakamega Forest, Kenya, were from the leaf litter layers. Similarly, de Winter and Gittenberger (1998) stated that the great variety in size, shape and firmness of leaves in Cameroonian rainforest, in conjunction with different rates of their decomposition determined by small-scale factors such as moisture and soil conditions, provides a wide range of microhabitats supporting high land mollusc diversity. These and other studies (Cameron *et al.*, 2005a) provide support for components of Solem's (1984b) world model of land snail diversity and abundance.

1.3. Iberia: a malacologically rich area

The majority of Iberia, and all of southern Iberia, lies in the Mediterranean bioclimatological region (Rivas-Martinez, 1973; André, 1984) (Figures 1.1, 1.2 and 2.1). This region is characterized by mild, moist winters and sunny, cloudless summers, with one or more months without rain (Suc, 1984; Polunin and Walters, 1985; Atlas Nacional de España, Anon, 1991-1995; Blondel and Aronson, 1999), although there are considerable local variations (Rivas-Martinez, 1981; Perry, 1997). Both Mediterranean and Eurosiberian

vegetational regions occur and these are partly determined by climate (Rivas-Martinez, 1987; Shoshany, 2000). The Mediterranean region is well suited for analyzing patterns and processes of diversity for two main reasons. First, the landmasses that encircle the Mediterranean Sea are parts of three continents: Europe, Africa and Asia, and this leads to biogeographical diversification. Second, the geological and vegetational diversities of habitats around or on the mountains, islands and peninsulas result in very diverse biotas (Blondel and Vigne, 1993; Richardson and Cowling, 1993; Lavorel and Richardson, 1999; Steinitz *et al.*, 2006).

Figure 1.1. Map of Iberia and surrounding regions (Image reproduced with permission of www.sitesatlas.com).



Iberia is one of the regions in Europe with highest species diversity (Ramos et al., 2001), with high floral (Polunin and Smythies, 1988; Giménez et al., 2004) and faunal (Bellés, 1990; Thompson, 1999) diversity, and high rates of endemism (Polunin and Smythies, 1988; Bellés, 1990; Moreno Saiz et al., 1998). This high diversity and endemism can be attributed in large part to the varied topography of the region that has provided suitable habitats through several glacial cycles (Alcaraz et al., 2006) and that has allowed the divergence and accumulation of genomes. Some species have maintained populations for many glacial cycles (Knowles, 2001; Branco et al., 2002; Zangari et al., 2006). This is in contrast to northern Europe where glacially-induced changes in the distributional ranges of taxa have resulted in less genetic variety than southern Europe in terms of number of species, subspecific divisions and allelic diversity (Solem, 1985; Hewitt, 2000; Hampe et al., 2003; Schmitt and Krauss, 2004).

The Pleistocene ice sheets did not cover the Mediterranean Basin (Panos et al., 1997; Valero-Garcés et al., 2004; Narciso et al., 2006), and Iberia, Italy and the Balkans were the main southern European refugia of the glacial periods (Hewitt, 2000; Sharbel et al., 2000; Seddon et al., 2001; Carrión et al., 2003; Habel et al., 2005). There is also evidence for postglacial recolonization from central Europe (Bilton et al., 1998; Lagercrantz and Ryman, 1990).

Past climatic fluctuations have caused changes in the demography and distributions of many species (Durand et al., 1999; Paulo et al., 2001; Aransayl et al., 2003; Pfenninger et al., 2003; Robledo-Arnuncio et al., 2005). The distributions of many European species changed as a result of populations moving northward from these refugia, and associated consequent population

Figure 1.2. Satellite images of Iberia. The upper image shows all Iberia, the lower image shows mid-southern Iberia with a part of Morocco. Images reproduced with permission of GEOsource World Guide (www.geosource.ac.uk).





interactions, during warming at the end of the Pleistocene (Walker, 1995; Hewitt, 1996, 1999; Taberlet et al., 1998; Hellberg et al., 2001). Postglacial colonization from glacial refugia may explain the present-day distribution of many European land molluscs (Hausdorf and Henning, 2004; Pinceel et al., 2005). Refugia may also have existed in parts of central Europe such as Hungary (Stewart & Lister, 2001; Deffontaine et al., 2005) and in western Asia (Bilton et al., 1998). Postglacial colonization from central Europe may have occurred through the Burgundian Gap, a corridor from north-eastern France to Germany (Hertelendy et al. 1992; Schmitt et al., 2002; Schmitt and Krauss, 2004).

1.4. Current status of research

Malacologically, Iberia (especially southern Iberia) with its high number of species, diversity and endemism of land molluscs (Sacchi, 1965; Puente et al., 1998), is not as well known as other parts of Europe (Bruggen, 1995; Wells and Chatfield, 1995). Most of the limited ecological work carried out in Iberia has been in the north (Outeiro and Hermida, 1995) and Iberia, as well as the Balkans, Greece and Turkey, are areas in Europe that Bruggen (1995) identified as sources of great diversity that are relatively un-worked, although recently there have been several detailed ecological studies from some of these areas (Cameron et al., 2000, 2003). In a review of non-marine mollusc conservation in Europe, Wells and Chatfield (1995) highlight the lack of data from southern European countries, which they argue have the highest diversities, endemism and greatest potential threats for diversity (see Stefanescu et al., 2004; Zavala and Zea, 2004; Butzer, 2005; Arndt et al., 2005; Lavergne et al., 2005; Rodríguez-Prieto and Fernández-Juricic, 2005; Zamora et al., 2007, for current

status in Mediterranean). They also state that the areas with highest species diversities are often those with fewest resources for malacological research.

The works of Hidalgo (1875, 1875-1884, 1890-1913) were monumental in their coverage of Iberian land molluscs. They are also an entry point for much of the early literature for the region. In his treatment of the literature relating to Valencia (which applies generally to other areas as well) Martínez-Ortí (1999) describes four main periods of malacological activity: the initial period (1821-1856, with contributions mainly from non-Spanish workers such as Albers, Morelet and Schmidt); the Hidalgo period (during which Hidalgo published many of his most important works); the intermediate period (during which important contributions from Spanish workers, such as Ortiz de Zárate, were made); and the modern period, beginning in the early 1960s.

Literature reviews related principally to taxonomy and systematics of parts of Iberia are in Manga Gonzalez (1983), Altonaga (1988), Bech (1990), Castillejo and Rodriguez (1991), Arrébola (1995) and Martínez-Ortí (1999). Many of the works by Sacchi (references in Sacchi, 1965) consider the malacofauna in a biogeographical context. Some of the problems discussed by Sacchi (1965), such as shell morphology in relation to ecology in *Iberus*, are still not elucidated (see Lopez-Alcantara *et al.*, 1985; Puente, 1994: Arrébola, 1995; Elejalde *et al.*, 2005; Gallego, 2006 for discussions on the generic status of *Iberus*).

Sacchi (1965) considered the study of Iberian land molluscs from ecological and historical bases. In this classic study he considered Iberia to be one of the most biogeographically interesting areas of Europe and saw the region as a bridge extending from France towards Morocco, isolated from

surrounding landmasses, with coastlines unchanged since the Miocene. Sacchi argued that Iberia's position between the Atlantic and the Mediterranean, and its complicated orography, contributed to climatic diversity. He considered the main zoogeographical regions of Iberia, and recognized the numerous European species and endemic species closely related to species from other European areas that do not cross the Ebro Valley, and so are limited to northern Iberia. Sacchi also indicated evidence for a Tertiary land bridge between the Spanish Betic Cordillera and the Moroccan Rif (the Betico-Rifian bridge) based on the malacofauna; evidence that has recently been elaborated and substantiated geologically (Medialdea et al. 2004; Sanz de Galdeano and Alfaro, 2004; Platt et al., 2005; Reicherter and Peters, 2005). He also showed that the calcareous Mesozoic chains of hills in moist Andalucia, furthest from the Mediterranean and Atlantic coasts, shelter some Moroccan species, confirming the essential character of this biogeographical zone as a migration route. There is also evidence of the introduction into Europe of land mollusc by humans (Guiller et al., 1994, 2006; Davies, 2008).

Other than habitat descriptions and rudimentary biogeographical analyses adjoined to taxonomic works (Altonaga, 1988; Puente, 1994; Arrébola, 1995; Martínez-Ortí, 1999) and a preliminary biogeographical study (André, 1984) there has been no research on the ecology of land molluscs in southern Iberia. Recently published papers have indicated the need for research from Mediterranean regions. Magnin *et al.* (1995) stated that studies of relationships between land snail communities and landscapes in the Mediterranean are scarce, and Labaune and Magnin (2002), who studied pastoral management and the dependence of land snails on plants and habitat structure, stated how little is

known about these areas of study for the Mediterranean region. Cameron et al. (2000) stated that garigue and maquis habitats (two of the main habitat types of the Mediterranean region, consisting mostly of herbaceous plants and shrubs of low to medium height) are widespread in the region and that data from different areas from the region could provide evidence on the structure of molluscan faunas.

A large number of studies have demonstrated relationships between the distributions and diversities of land molluscs and large-scale factors such as climate, geology and habitat type (Section 1.2). Some of these factors determine distribution and abundance in the malacofaunas of many regions. In common with other taxa (Tews *et al.*, 2004), very little is known, however, about how important factors are at small scales, for example 50x50m, and almost nothing at all about the effects of scale on these relationships.

There are now several studies that have been conducted at sites of 1km², often using smaller plots within these (generally 20x20m or 40x40m), to assess land mollusc species diversities. The first studies of this kind were from rainforests, which are among the most vegetationally species-rich habitats (Aiba et al., 2004), and tested the comment made by Solem (1984b) that in rainforests: 'Snails may be abundant on ecotonal fringes, but generally are neither diverse nor abundant'. There are recent studies from a few Mediterranean areas that all use the same scales and methods, and so allow comparison of data (Section 4.5.3). This present study uses similar scales, and other data are beginning to accumulate from different regions, some quite distant from one another, using comparable sampling units. These data may provide the beginnings of a

quantitative model to explain the distributions and diversities of land molluscs at different scales (Solem, 1984b; Gardner, 1998).

The effects of area and of habitat structure have been extensively studied for many taxa. Numerous models have been proposed to explain these effects (Sections 5.2 and 5.3). There are very few studies that have specifically looked at how area and habitat structure affect land molluscs, and almost no quantitative data exist. A difficulty with assessments of this kind has been that different elements of structure (e.g. vegetation, soil and rocks), and quantities of these, are often confounded making it difficult to compare results between studies.

A habitat structure model proposed by McCoy and Bell (1991) has three axes that take account of ecological relationships that are affected by habitat structure (Section 5.3). These three axes are heterogeneity (types of structure, such as rocks and vegetation), complexity (quantities of structure) and scale (size of area used to measure heterogeneity and complexity). This model allows the effects of habitat structure to be teased out and quantified across various scales at the same locality, the results of which can then be compared to other localities. This, in conjunction with data for assessing effects on distribution and diversity from a larger area (a region), may provide a solid basis for determining factors that affect land molluse diversity. This is the approach in this study.

1.5. Aims of this study

This is the first ecological study of southern Iberian land molluscs and its main aims and objectives are:

1. To provide a preliminary biogeographical survey of the land molluscs of southern Iberia.

- 2. To determine the factors that affect the distribution and diversities of land molluscs in the region and assess diversity in relation to other regions.
- 3. To assess the effects of habitat heterogeneity and complexity on the number of species and species abundances at three scales (1m², 5m² and 20m²) in three habitat types, and to determine if these effects are scale-dependent and habitat-specific.
- 4. To assess the number of species, species abundances and environmental variables at three scales (1m², 5m² and 20m²) in three habitat types, and to determine if there are variations in these in relation to the wet and dry periods of the year.

Southern Iberia is particularly suited for carrying out such a study because there is high species diversity, and the region is heterogeneous with a broad range of habitat types such as steppe and garigue that are highly suitable for testing hypotheses about habitat structure effects on diversity. In addition, carrying out the study in southern Iberia is particularly important because:

- Very little is known about the malacofauna of the region and the study will provide the first detailed data for this region.
- Parts of the region are under threat from development and there are no data available on the molluscs that are endangered or at risk from many of these areas.
- 3. The data will be available for comparison with data recently published from other Mediterranean countries (e.g. Cameron et al., 2000, 2003;

Labaune and Magnin, 2001). This will enable a more detailed picture to emerge of the malacofauna from the Mediterranean region.

4. The data will allow comparisons of the southern Iberian malacofauna with the North African malacofauna. This will be used as part of the research being done by the author and others in the Interreg programme of collaboration with Morocco (GIBMANATUR) that will involve the comparative sampling of sites for land molluscs and environmental factors from both regions.

The aims of this study require that analysis of pattern and process of distribution and diversity in southern Iberian land molluscs be carried out at two very different scales. The thesis is divided into two Parts, reflecting this requirement. In Part One biogeographical patterns are assessed by sampling 1km² sites from Guardamar del Segura in eastern Spain, to Lagoa de Santo André in Portugal, an extent of about 1500km. Molluscs are sampled by direct searching at the sites, and by sieving soil. Data are analysed using univariate and multivariate methods to determine species distributions and diversities, and to find factors that explain patterns in these.

In Part Two sites are sampled at a much smaller scale. A nested method is used to assess the effects of habitat heterogeneity and complexity on species diversities in sand, steppe and garigue habitats at 1m², 5m² and 20m². The sampling allows relationships between species and environmental data to be studied in detail, assessment of possible changes across the three scales to be made, and specific hypotheses about habitat structure to be tested.

Findings from each of these two approaches to studying land molluscs and their environments are discussed at the end of each part. A general discussion at the end of the thesis examines themes related to both approaches and attempts to synthesize the main findings in the context of current research in land mollusc ecology.

Part One: Biogeography

CHAPTER 2. INTRODUCTION

2.1. Malacology and Biogeography

Over 20 years ago Solem (1984a) wrote that malacologists were not at the forefront of biogeographical studies. There has since been a clearer understanding of what biogeography should encompass as a discipline and most definitions state that it involves the study of the geographical distributions of organisms (Cox and Moore, 1985; Lincoln *et al.*, 1998). A distinction is made between the study of ecological processes that occur over short periods of time, and which act on distributional patterns, and the study of processes that act over longer periods (millions of years) to influence patterns of distributions. The former is referred to as ecological biogeography, the latter as historical biogeography (Crisci *et al.*, 2003; Lunt and Spooner, 2005; Bueno-Hernández and Llorente-Bousquets, 2006).

Recent trends have moved from more narrative biogeographical methods towards more analytical approaches that have rigorous inferences. These show that the distributional patterns of organisms are not the result of a single cause, whether ecological or historical (Myers and Giller, 1988; Crisci, 2001), and that a combined approach is more appropriate (Crisci et al., 2003; Posadas et al., 2006) supported by phylogeographical studies which attempt to identify the mechanisms influencing the geographical distributions of phylogenies in closely related species (Avise, 2000, Hugall et al., 2003). These concepts have been highlighted in a recent review of historical biogeography and ecology (Wiens and Donoghue, 2004) that identifies the divide between research into ecological and historical processes influencing species distributions, and how integrating

these approaches can help to explain patterns in community assembly and species richness patterns.

Buffon (1761) postulated that different regions of the world were inhabited by different species of plants and animals. There have since been many attempts to characterize the major areas of the world based on their flora and fauna. This was the approach of Wallace (1860, 1876) who based his zoogeographical divisions mostly on birds and mammals, although these have also served as a framework for floral divisions (Bates, 1990). A detailed classification based on faunas was published by Schmidt (1954) and this has formed the basis for many other classifications.

Pielou (1979), pointing out that the methods used for these classifications were subjective, approximately representing the consensus of biogeographers from various specialities, described an objective method to classify biogeographical areas based on divisive information analysis as used by Kikkawa and Pearse (1969). Objective methods of analysis have been used for birds (Williams *et al.*, 1999), plants (Qian, 2001; Kingston *et al.*, 2003) and bats (Procheş, 2005). Vegetation types and climate have also been used to define biogeographical regions (Olson *et al.*, 2001) (Table 2.1). The subjective approach is still widely used to divide the world into biogeographical regions and has been used to define major land mollusc regions (Abbott, 1989, Table 2.2).

Table 2.1. Biogeographical regions of the world according to Wallace (1876), Pielou (1979) and Proches (2005).

Wallace (1876)	Pielou (1979)	Procheş (2005)
Australian	Australasian	South and Central America
Ethiopian	Ethiopian	Caribbean
Nearctic	Nearctic	Patagonia
Neotropical	Neotropical	North America
Oriental	Oriental	New Guinea
Palaearctic	Palearctic (sic)	Melanesia
	Oceanian	Australia
	Antarctic	Tropical Asia
		Africa
		Madagascar
		Temperate Eurasia

Table 2.2. The main land mollusc regions according to Abbott (1989).

Region	Description	
Holarctic	Cold to temperate. From North America to northern Mexico, Europe and northern Africa. Asia north of the Himalayas. Divided into Palaearctic (Europe and Asia), Nearctic (North America). Exchange of genera and species in families Cochlicopidae, Valloniidae and Helicidae. In the eastern United States Polygyridae and Haplotrematidae are common; the subfamilies Oreohelicinae, Sonorellinae and Humboldtianinae are found in the western United States. In the warmer Mediterranean areas of the Palaearctic the Clausiliidae and Hygrominae are common.	
Neotropical	New World tropical and subtropical parts of Mexico, Central America, West Indies and South America. Prosobranchs are common, as well as Strophocheilidae, <i>Polymita</i> and <i>Liguus</i> .	
Oriental	India, Sri Lanka, southern China, and Japan, southeastern Asia and eastern Indonesia. Dominant groups include: Camaenidae, Acavidae, Helicostylinae and Bradybaeninae.	
Ethiopian	Africa south of the Sahara and the nearby Indian Ocean islands such as Seychelles and Madagascar.	
Australian	Australia, western Indonesia, New Guinea, Melanesia, New Zealand. Unique genera such as <i>Papuina</i> and <i>Placostylus</i> are present.	

Malacologists are now much more engaged in biogeographical studies than 20 years ago and there are detailed biogeographical studies for regions including eastern North America (Nekola, 2005), northern Europe (Pokryszko and Cameron, 2005) and New Zealand (Barker and Mayhill, 1999; Barker, 2005). There are also biogeographical studies of some molluscan taxa (which sometimes include phylogeographical analyses) that have helped elucidate the processes that account for distributions. Hausdorf (1995) showed that dispersal

across barriers, rather than vicariance events, explained the distribution of Stylommatophora in Sundaland, southeast Asia. In a study of present-day world distributions of Vitrinidae, Hausdorf (2001) concluded that ecological displacement or exclusion of vitrinids by slugs is probably due to competition for shelter. Other works have focused on the origins, and dispersal, of taxa with wide distributions. Scott (1997) investigated the biogeography of the Helicoidea and concluded that the vicariance patterns for the superfamily indicates that families originated with the splitting of eastern Gondwana and Laurasia between the late Mesozoic and mid-Tertiary.

Biogeographical studies from the Mediterranean, however, are scare. Sacchi (1977, 1984) defined a biogeographical limit to *Cepaea nemoralis* (Linnaeus, 1758) and *C. vindobonensis* (Férussac, 1821) along the Adriatic coasts of Italy based on their distributions and ecological factors; Welter-Schultes (2000) studied the patterns of geographical and altitudinal variation in *Albinaria* from Crete, and Uit de Weerd (2005) reported on the biogeography of Greek Clausiliidae. A recent study by Madec *et al.* (2003) reports that characters used to differentiate populations of *Cantareus aspersus* (Müller, 1774) in the western Mediterranean correlate with geography but that shell size between populations is often influenced by local conditions, illustrating the high degree of phenotypic plasticity of this species (Guiller *et al.*, 1994; Arnaudl *et al.*, 2003).

Biogeographical analyses of non-molluscan, Circum-Mediterranean taxa (including flies, crane flies, scorpions, frogs and newts) have shown that the oldest faunal elements in the western Mediterranean date from before the Miocene, with the origin of younger lineages linked with the Late Oligocene-

Early Miocene formation of a landmass separating the Tethys from the Paratethys. Major divergence may have resulted by subsequent vicariant and distributional events throughout the Mediterranean during the Miocene (Oosterbroek and Arntzen, 1992).

Gantenbein (2004) assessed the genetic population structure of the scorpion *Buthus occitanus* (Amoreux, 1789) in the western Mediterranean (specifically in the region of the Strait of Gibraltar). Phylogenetic analysis based on estimated gene frequency data resulted in a cladistic tree that divided the populations into three clades: European, Atlas (Morocco) and Tell-Atlas (Tunisia). Cossan *et al.* (2005) have shown that an over water dispersal event explains the phylogeographical structure of greater white-toothed shrew populations on either side of the Strait of Gibraltar. Other similar studies have demonstrated that this Strait has separated the Iberian fauna from the Mahgrebian (North Africa) fauna and has been a geographical barrier to gene flow during the last 5 million years (Busack, 1986; Palmer *et al.*, 1999; Palmer and Cambefort, 2000).

2.2. The malacofauna of southern Iberia

2.2.1. Biogeography

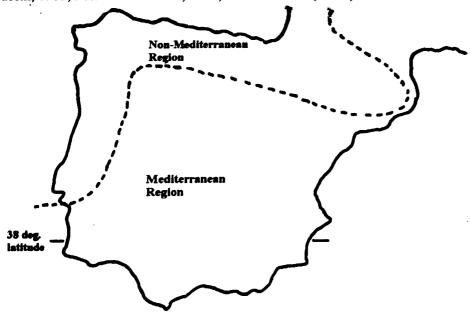
Attempts to define major biogeographical regions in Iberia have been based on various taxa including earthworms (Rodríguez et al., 1997), beetles (Gallego et al., 2004) and plants (Rivas-Martinez, 1987). Hidalgo (1875), who divided Iberia into five regions qualitatively based on the distributional patterns of species, was the first to undertake a biogeographical study of Iberian land molluscs (Section 1.4). There have since been several more detailed and quantitatively-derived biogeographical assessments (Table 2.3).

Table 2.3. The main biogeographical studies of land molluscs in Iberia. The original terminology, and spelling, of the regions by the authors have been retained.

Regions used to divide Iberia	Source
Cantabrica, Pirenaica, Castellana, Betica, Valentiana	Hidalgo, 1875
Galiciana, Cantabrica, Pirenaica, Aragonesa, Iberica, Castellana, Carpetana, Extremadura y la Mancha, Levantina, Betica, Sur-Oriental, Penibetica	Cereceda, 1957 in Hermida et al., 1994
Spanish Levante, eastern Andalusia, Moist Andalusia, Guadalquivir plain, Portugal and Galicia, eastern Balearics	Sacchi, 1965
Cataluña, Aragon-Cataluña, Levante, Almeria, Andalucia, Este de Castilla, Oeste de Castilla, Palencia- Burgos, Badajoz, Alentego, Algarve	André, 1984
Basque-Pyrenean-Catalonian, Castilla la Vieja, Mediterranean, Extremadura-LaMancha-Andalusia, Lusitanian	Puente, 1994; Puente et al., 1998

Despite some inconsistencies in the identification of biogeographical regions resulting from these studies they do, in general, identify a major divide in Iberia between the Mediterranean and non-Mediterranean (Atlantic) regions (Figure 2.1). This divide, as detailed by Sacchi (1965), begins in the southern slopes of the Catalonian Pre-Pyrenean Mountains, continues to the central Pyrenees, then to the Cantabrian Mountains to Galicia, and onto northern and central Portugal.

Figure 2.1. Iberia. The dotted line shows the divide between the Mediterranean and non-Mediterranean (Atlantic) regions. Also shown is the position of 38° latitude (adapted from Sacchi, 1965; Polunin & Walters, 1985; Rivas-Martinez, 1987).



Arrébola et al. (2004a, b) used geographical districts and provinces (comarcas and provincias) to characterize human collection and consumption of land snails in Andalucia.

Table 2.5. The number of species, Andalucian and Iberian endemics, in the biogeographical regions of Andalucia, southern Iberia. The regions are those used by Arrébola (2002) and are based on Ibarra Benlloch (2003) who includes a further region, the Algarriense. Data adapted from Arrébola (2002). ¹Andalucian endemics are species found only in Andalucia. ²Iberian endemics are found in other areas of Iberia but have their main distributions in Andalucia.

Biogeographical region	Number of species	Andalucian endemics ¹	Iberian endemics ²
Hispalense	36	1	1
Rondeño	31	6	2
Malacitano-Almijarense	54	6	2
Sub-Bético	29	3	2
Alpujarreño-Gadorense and Nevadense	16	1	1
Guadiciano-Bacense and Manchego	18	1	1
Aljíbico	46	8	1
Gaditano-Onubense	31	0	1
Mariánico-Monchiquense	34	0	4
Almeriense	20	5	0

2.2.2. Diversity

Magurran (2004) has pointed out that following the review of Hurlbert (1971) many ecologists used the term diversity only when referring to quantitative measures that combine species richness and evenness (such as the Simpson's and Shannon indices), but that in the last 10 years this practice has diminished as popular interest in biological diversity grows (Nobis and Wohlgemuth, 2004). Diversity, as well as biological diversity, are now considered by many to be synonymous with number of species (see also: Allaby, 2004; Lincoln *et al.*, 1982, 1998; Magurran, 1988). For clarity, in this study the term diversity is used when reference is made to measures that combine number of species and evenness, and number of species is used when referring to the number of species present (i.e. *sensu* Hurlbert, 1971).

Recent estimates of the total number of species of land molluscs for Europe, which includes the Atlantic Islands and areas of the Mediterranean, range from about 3,000 (Wells and Chatfield, 1995) to 3,600 species (Cameron et al., 2005b). The numbers of species from regions and countries that have received the attention of malacologists for many years are known fairly accurately (Table 2.6); these include Britain and Ireland (Kerney, 1999), France (Falkner et al., 2002) and Malta (Giusti et al., 1995). Approximations of number of species are available for some countries (Wells and Chatfield, 1992, 1995), but not for Iberia as a whole, although Puente (1994) reports a total of 141 species of Helicoidea (of which 87 are endemics). The definitive work for Iberian land molluscs will be the volume in the Fauna Iberica Monograph series to be published by the Museo Nacional de Ciencias Naturales, CSIC (Madrid), but this is still a number of years away (Ramos et al., 2001; Jose Arrébola, pers. com.).

Table 2.6. The numbers of species of land molluscs from different regions and countries. Note: * indicates that the totals include freshwater as well as land species (sources: Giusti et al., 1995; Wells and Chatfield, 1995; Barker and Mayhill, 1999; Cameron et al., 2000; Falkner et al., 2002; Cameron, 2004; Aravind et al., 2005; Menez, 2005).

Country	Number of species	Country	Number of species
Gibraltar	41	Netherlands	102
Malta	56	Norway	134*
New Zealand	1400	Finland	68
Tasmania	65	Ireland	93
Japan	740	Canary Islands	181*
Italy	~400	Belgium	117
Iceland	26	Slovakia	160
Scandinavia	116	Hungary	148
Denmark	87	Turkey	550
Greece	~600	Israel	96
British Isles	126	Madeira	237*
Azores	98*	Switzerland	196
Sweden	~200*	Germany	190
Poland	162	Austria	224
Romania	295	France	256
Albania	225	India	1488

The few studies that have been undertaken in southern Iberia consist of species lists (Table 2.7). Values for diversity indices are very rarely reported and, in the absence of densities, cannot be calculated from these studies.

Table 2.7. Studies of diversities of land mollusc species from southern Iberia.

Location	Number of sites/samples	Number of species	Source	
Sevilla	30	29	Arrébola (1990)	
Andalucía	228	64	Arrébola (1995)	
Comunidad Valenciana	910	106	Martínez-Ortí (1999)	
Sierra de Alcaraz, Albacete	29	47	Martínez-Ortí et al. (2004)	
Southern Iberia	91	94	This study	

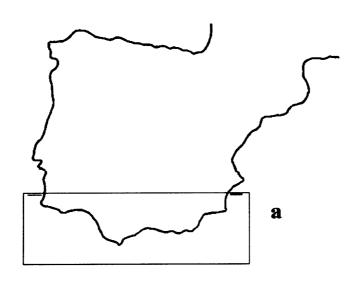
The main aim in Part One is to determine the factors that affect the distribution and diversities of land molluscs in southern Iberia, and to assess diversity in relation to other regions (Section 1.5). Univariate and multivariate methods including diversity indices, species abundance models and cluster analysis are used for this.

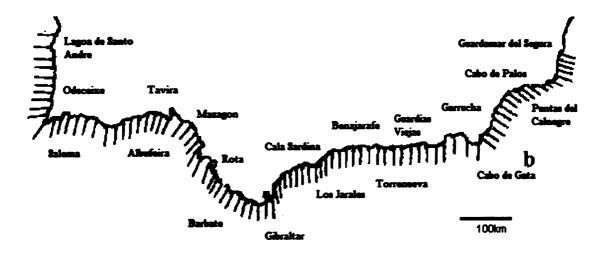
CHAPTER 3. METHODS

3.1. The study area

The study area is southern Iberia, defined in this study as the part of the Iberian Peninsula below the 38° line of latitude, and which includes Gibraltar, southeast Spain and southern Portugal (Figure 3.1).

Figure 3.1. Iberia (a) showing extent of the 38° line of latitude (box) and detail of boxed area used for this study along the coast of southern Iberia (b). Each marker indicates the position of a site, from Guardamar del Segura, Spain (top right) extending clockwise along the coast to Lagoa de Santo André, Portugal. These sites extend approximately 1500km along the coast. (See Appendix 1 for details of sites and Appendix 2 for photographs of sites).





3.2. Selection of sites

The aim was to have a site every 10-15km along the 1500km stretch of coast in southern Iberia (Figure 3.1, Appendices 1 and 2) encompassing as large a geographical area as possible. A linear-type system (using segments for site selection, see below) was determined to be the best way to achieve this. The following criteria were met by the sites:

- (1) an area of approximately 1km² with no man-made structures, or only a minimal number of these,
- (2) a distance of not more than 5km from the coast (to keep sites within the segments used (see below) and to standardize, as far as possible any effects on the data because of proximity to the coast),
- (3) an area with as little anthropogenic disturbance as possible (visual assessment of buildings, roads, other construction etc.), and
- (4) an area with as much habitat variation as possible, e.g. garigue, steppe, etc. (visual assessment).

Segments were drawn on a map (Figure 3.2) and then a site nearest the centre of each segment that met the required criteria was sampled (Figure 3.3; Drinnan, 2005). The suitability of each site was determined in the field based on the criteria listed above. This sometimes resulted in the site for a particular segment being located away from the centre, and because of this it was not possible to have sites equally spaced along the 1500km of coast. This constitutes a one-stage stratified sampling method with the segment being the stratum (Bart *et al.*, 1998; Dytham, 1999). Ninety-one sites were sampled for Part One of this study (details in Appendix 1).

Figure 3.2. Detail of a part of the map used to select the Biogeographical Sites using the segment method. Dashed lines delimit segments. See Figure 3.3 for a stylized representation of the segment method.

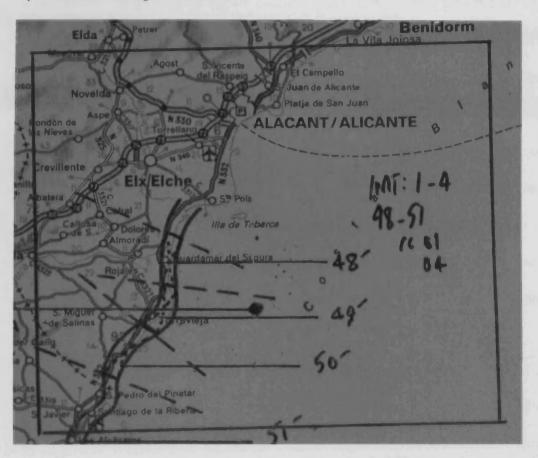
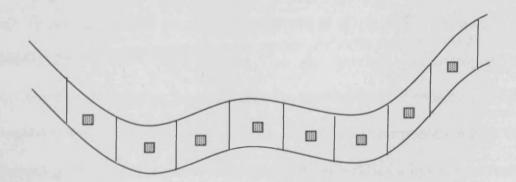


Figure 3.3. A stylized representation of the segment method used to select the Biogeographical Sites. Each segment (delimited by vertical lines) includes a site (stippled square) that is selected based on pre-assigned criteria (see text for further details and Figure 3.2 for part of the map used).



3.3. The sampling periods

A year in the Mediterranean region can be climatically divided into the dry and wet periods (Schimper, 1903; Cody and Mooney, 1978). The dry period is generally considered to be from the end of May to September, and the wet period from October to the end of May (Blondel and Aronson, 1991; Font Tullot, 2000; Aviad *et al.*, 2004). Biological resources, such as water, soil nutrients and plant biomass, typically go through periods of high and low abundance (Schwinning and Sala, 2004; Sher *et al.*, 2004), and many species of plants and animals show physiological and behavioural adaptations to these periods (Blondel and Vigne, 1993; Faulkner and Hill, 1997; Blondel and Aronson, 1999; Grove and Rackham, 2001; Schwinning *et al.*, 2004).

Many land molluscs exhibit decreased activity during the dry period in the Mediterranean region (Bar and Mienis, 1979; Giokas et al., 2005). Heller and Ittiel (1990) reported decreased activity in Helix texta Mousson, 1861 from Israel during the dry period, and Parmakelis and Mylonas (2004) reported inactivity in Mastus butoti (Maassen, 1995) and M. cretensis (Pfeiffer, 1846) during the dry period in Crete. Other taxa, both vertebrate and invertebrate, have activity patterns related to seasonality (Rueda et al. in press). Stamou et al. (2004), for example, have shown that the survival of arthropods in Mediterranean conditions involves specific combinations of conservative and conformist traits, and that the population dynamics of arthropods follow the seasonality of the Mediterranean climate. Extensive fieldwork in southern Iberia by the author has shown that sampling for molluscs in the wet period generally maximizes the number of species that can be found at a site. To maximize the

number of species found at all sites sampling was carried out during the wet period.

3.4. The environmental variables

In this study environmental variable is defined as any variable that is measured for its possible effects on the numbers, abundances and distributions of species at sites (Lepš and Šmilauer, 2003). The definition thus includes biotic and environmental (i.e. abiotic) factors (Clarke and Warwick, 1994; Lincoln et al., 1998; Jones and Reynolds, 1996). The species data are the primary data set sensu Lepš and Šmilauer (2003) with individual species being response variables.

Large-scale environmental variables were measured because of the large extent of the geographical area considered in Part One of the study, as well as the size of the sites (1km²). These, being mostly climatic and geological variables, would not be expected to have high variance at the scale at which the sites were sampled. Variables such as pH and calcium content of soil were not measured as the high heterogeneity at the sites (that contained more than one habitat type, Section 3.2) would have required extensive replication of this type of variable to adequately provide an indication of their variance at the sites. The variables measured at the sites and the scoring criteria used for the classification of the rocks/deposits and geological periods are detailed in Tables 3.1, 3.2 and 3.3.

Values for climatic variables were assigned to sites based on the data mapped in Daveau (1977, 1985), Albuquerque and Nunes (1978), Font Tullot (1984, 2000) and Anon. (1991-1995). Data for each site was derived from the mapped data by matching site positions to the climatic maps. Data from

meterological stations adjacent to sites would have provided data more closely related to the sites. These data were largely unavailable because of the paucity of meterological stations in the study area.

Table 3.1. The environmental variables measured at the Biogeographical Sites. Key: ¹DV=diurnal variation (the difference in means between maximum and minimum daily temperatures), ²00=mean number of days in year with recorded temperature less than or equal to 0°C, ³20=mean number of days in year with recorded temperature more than or equal to 20°C. (Sources: Daveau, 1977, 1985; Albuquerque and Nunes, 1978; Font Tullot, 1984, 2000; Anon., 1991-1995, 1994).

Variable	Classification/unit of measurement
Altitude	Metres above sea level (using altimeter)
Geology (rock/deposit type)	sensu Roberts, 1989; Anon., 1994 (see Table 3.2.)
Geological period	sensu Black, 1998; Lincoln et al., 1998 (see Table 3.3.)
Rainfall	Annual mean (mm)
Sunshine	Annual mean (hours/day)
Sunshine-January	Monthly mean (hours/day)
Sunshine-February	Monthly mean (hours/day)
Sunshine-March	Monthly mean (hours/day)
Sunshine-April	Monthly mean (hours/day)
Sunshine-May	Monthly mean (hours/day)
Sunshine-June	Monthly mean (hours/day)
Sunshine-July	Monthly mean (hours/day)
Sunshine-August	Monthly mean (hours/day)
Sunshine-September	Monthly mean (hours/day)
Sunshine-October	Monthly mean (hours/day)
Sunshine-November	Monthly mean (hours/day)
Sunshine-December	Monthly mean (hours/day)
Temperature	Annual mean (°C)
Temperature-January	Monthly mean (°C)
Temperature-July	Monthly mean (°C)
Temperature (DV)¹-January	Monthly mean (°C)
Temperature (DV) ¹ -July	Monthly mean (°C)
Temperature $(00)^2$	Annual mean (number of days)
Temperature (20) ³	Annual mean (number of days)
Wind velocity	Annual mean (km/hour)
Absolute humidity	Annual mean (g/m³)

Table 3.2. The scores used for the geological classification of the principal rocks/deposits at the sites according to data in Anon., 1994 (Mapa Geológico de la Península Ibérica, Baleares y Canarias). Terminology based on Roberts, 1989 and Anon., 1994.

Score	Geological classification of rocks/deposits
1	Plutonic rocks
2	Metamorphic rocks
3	Conglomerates, Sandstones, Slates, Calcites
4	Conglomerates, Sandstones, Slates, Gypsum, Clays
5	Slates, Dolomite, Marl, Conglomerates, Sandstones
6	Slates, Dolomite, Marl, Sandstones
7	Conglomerates, Sandstones, Clays, Calcites, Evaporites
8	Calcareous turbidites
9	Conglomerates, Sandstones, Clays, Slates, Evaporites
10	Conglomerates, Gravels, Sands, Muds

Table 3.3. The scores used for the geological Eon, Era, Period or Epoch of the principal rocks/deposits at the sites according to data in Anon., 1994 (*Mapa Geológico de la Península Ibérica, Baleares y Canarias*). Terminology based on Anon., 1994 and Lincoln et al., 1998.

Score	Geological Eon, Era, Period or Epoch	Geological time (millions of years before present)
1	Proterozoic-Palaeozoic	2400-245
2	Palaeozoic-Triassic	570-210
4	Carboniferous	365-290
5	Triassic	245-210
3	Mesozoic	245-65
6	Jurassic	210-140
7	Cretaceous	140-65
8	Cretaceous-Palaeocene-Eocene	140-38
9	Palaeocene-Eocene	65-38
10	Oligocene-Miocene	38-5
11	Miocene	26-5
12	Pliocene	5-1.6
13	Pliocene-Pleistocene	5-0.01
14	Pleistocene	1.6-0.01
15	Holocene	0.01-present

3.5. Sampling the land molluscs

The standardization of sampling effort and sample size are important considerations in the design of ecological studies (Southwood, 1978; Schneider, 1994; Bart et al., 1998; Magurran, 2004) but sampling effort is rarely documented in studies (Gaston, 1996a). Most land mollusc studies do not include an assessment of the time needed to find most species at a site, nor of the volume of substratum needed to find most of the species contained in the substratum (Menez, 2001). This situation may change as issues of sampling efficacy in land mollusc research become more topical (Cameron and Pokryszko, 2004, 2005; Section 8.1).

Analyses of diversity and habitat relationships have sometimes been based on, or have included, qualitative methods (Barker and Mayhill, 1999; Craw, 2001). Bishop (1977), and more recently Menez (2001, 2002a), discussed the use of quantitative sampling techniques for land molluscs and for the

recording of environmental variables in land mollusc studies. Various sampling methods have been used for land molluscs (Table 3.4).

Table 3.4. A selection of sampling techniques for land molluscs. The total number of species from each study is given (because number of sites and sampling methods differ among the studies, the total number of species between the studies are not directly comparable).

Region/area/locality	Method(s)	Total species	Source
South Downs, England	44 sites of 1000m ² . Direct search for 1hr. About 1.51 soil and litter.	· 43	Cameron, 1973
Granada, Spain	176 sites direct search, 5 to 100m ² , 1-1.5kg soil.	21	Alonso, 1977
Hel Peninsula, Poland	Litter and soil samples of 0.0625m ² . Total 256 samples.	10	Umiński and Focht, 1979
Vancouver Island, British Columbia	38 sites of 900m ² . Direct search 1hr. 51 litter per site.	26	Cameron, 1986
Madrid, Spain	68 samples, 0.5m ² topsoil only (no direct search).	15	Outeiro <i>et al.</i> , 1993
Northwestern Spain	60 sites of 100km ² . Direct search. 0.5m ² quadrats for soil collection to 5cm depth, 3 samples per site.	87	Hermida <i>et al.</i> , 1994
Hawaii	58 sites. 0.5m ² area sampled in 1h (or more). 15min looking at trees/shrubs. Litter/soil from 900cm ² at 5 sites.	16	Cowie <i>et al.</i> , 1995
Maubec, Luberon, France	Plots of 156.25 m ² .	33	Magnin <i>et al.</i> , 1995
Southeastern Madagascar	48 plots each 400m ² at 16 stations. Direct search of 3 person hours per plot. 81 of litter and soil plus litter sample per plot.	87	Emberton et al., 1996
Kakamega Forest, Kenya	31 plots 1600m ² . Direct search for minimum of 30min per plot, some plots with 3 people. 41 litter per plot.	53	Tattersfield, 1996
Southeastern Madagascar	16 stations, 3 1600m ² plots per station. Each plot sampled for 30min by 6 people. 81 leaf litter and 81 of soil plus leaf litter.	80	Emberton, 1997
Eastern Tanzania	12 stations. 2-4hr direct search in each.	159	Emberton et al., 1997
Northern Madeira	51 samples (sites). Direct search for about 30 min by 2 people. About 51 soil and litter.	84	Cameron and Cook, 1998
Cameroon	36 400m ² plots searched for 1hr each. About 41 of litter per plot. At many plots under storey vegetation (about 0.75-3m) was beaten. Tree trunks searched for about 30min.	97	de Winter and Gittenberger, 1998
Pukeamaru, northeastern New Zealand	23 sites of 2500 m ² . Direct search. Litter and humus (vol. unknown).	105	Barker and Mayhill, 1999
Great Lakes Region, USA	349 sites of 100 -1000m ² . Direct collection, 41 soil.	120	Nekola, 1999

Table 3.4 (continued).

Region/area/locality	Method(s)	Total species	Source
Southwestern Madeira	80 sites. 900m ² , 2 people for 30min to 1hr. 51 of litter and soil.	97	Cameron and Cook, 2001
Naxos, Crete and Peloponnese Islands	35 sites of 10 000m ² . Direct search for about 1hr by 3 people. About 51 of litter and soil from at least 5 locations at each site.	90	Cameron et al., 2000
Tutuila, Ta'ū, Ofu, American Samoa	Separate samples from vegetation and ground. Area of about 50m dia. 3 people searched veg for 20min. 1 person searched veg for 10min and ground for 10min. Extra non-quantitative samples collected along transects.	60	Cowie, 2001
Luberon, France	80 sites at each 25m ² plot searched for 15min by 2 people. 5 samples of 25cm ² each of veg, litter, soil down to 5cm in each plot of 25m ² .	32	Labaune and Magnin, 2001
Sabah, Malaysian Borneo	36 plots 400m ² each in a 1km ² area. 2 person hours per plot. Direct search. Beating of plants. 41 of litter per plot.	61	Schilthuizen and Rutjes, 2001
Mount Kenya, Kenya	64 plots of 4900m ² . Direct searching for 2.5 hours and 41 of soil and litter collected per plot.	68	Tattersfield et al., 2001
North Ronaldsay, Orkney	17 sites from 400 to 10000m ² direct search for at least 1hr. Litter and soil (?vol).	23	Cameron, 2002b
Luberon, France	80 sites each 25m ² . 15min per plot direct sampling. 5 samples of 625cm ² in each plot for litter and soil down to 5cm.	32	Labaune and Magnin, 2002
Stroumboulas, Crete	14 plots of 400m ² searched for 1h by 2 people. 4l topsoil sifted.	27	Cameron et al., 2003
Province, southeastern France	74 plots each 25m ² . 30min direct sampling per plot.	21	Kiss and Magnin, 2003
Arabuko Sokoke Forest, Kenya	10 plots of 1600m ² at each of 3 forest types. 1hr direct searching by 2 people. 4l per person (i.e. 2x4l) from each plot.	25	Lange and Mwinzi, 2003
Białowieża Forest, Poland	4 sites, 400m ² plot at each. Direct searching for 2 hours, collection of 10l of litter.	51	Cameron and Pokryszko, 2004
Southwestern Germany	83 sites of 100m ² . 4 plots representing 0.25m ² per site with removal of litter and soil to 3cm depth.	52	Martin and Sommer, 2004
Sabah, Malaysian Borneo	6 sites, 400m ² plot at each. Direct searching for 2 hours, collection of 51 of litter and soil.	74	Schilthuizen et al., 2004
Southeastern France	209 sites of 25m ² . Direct search and collection of soil and litter to 5cm depth.	87	Aubry <i>et al.</i> , 2005
Central Sweden	29 sites of 100m ² . 0.5m ² total area sampled from pooled samples.	20	Hylander et al., 2005

Table 3.4 (continued).

Region/area/locality	Method(s)	Total species	Source
Southern England	4 sites, 400m ² plot at each. Direct searching for 2 hours, collection of 10l of litter.	57	Cameron <i>et al.</i> , 2006
Israel	27 sites of 1km ² , each sampled using nine plots of 100m ² , each plot searched for 12 minutes.	50	Steinitz <i>et al.</i> , 2006

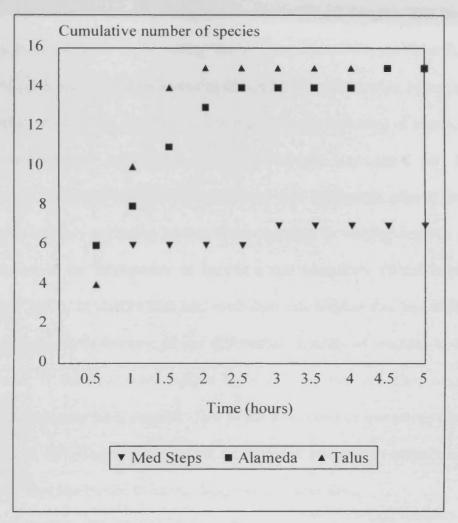
Two sampling methods were used: (1) direct search, and (2) collection of specimens from the soil. Sampling was carried out during the day. Most species, however, are nocturnal and are mainly active during the night up to early morning (Asami, 1993). Ward-Booth and Dussart (2001) showed that there were no significant differences in the number of species nor abundances of snails found in day and night sampling from an agricultural area of southeast England. In Mediterranean habitats, however, night-time searching remains the optimal strategy for land mollusc work (unpublished data), and it is recognized that values for number of species and abundances may have been different had the fieldwork been conducted at night. These differences would, however, be expected to be minimal because thorough searching under rocks, logs and other types of shelter will locate molluscs during the day. Fieldwork was not undertaken at night because of the difficulties this would have entailed, including adequate access and searching of sites, and safety issues related to the habitat types sampled.

3.5.1. Direct search

The direct search method is widely used for determining the abundances of species (Southwood, 1978; Sutherland, 1996; Table 3.4). The method involves the active search by eye for land molluscs on the soil surface, under rocks and logs, on vegetation etc., and the counting and/or collection of these. Ward-

Booth and Dussart (2001) found that this method is suitable for land snails, especially where more destructive methods cannot be used. The method has been used in a large number of land mollusc studies (e.g. Cook, 1984;

Figure 3.4. The species-time relationships for three sites representing three Mediterranean habitat types: Med Steps=maquis (dense, mostly evergreen shrub communities 1-3m high, Polunin and Walters, 1985); Alameda=man-induced (gardens); Talus=coastal (sand). At each site direct searching was used to collect all molluscs (including slugs) for 30-minute periods. Ten consecutive 30-minute periods of direct search sampling were carried out at each site for a total of 5 hours sampling at each site. The mean time at which asymptotes are attained is 2.5 hours, which indicates that adequate sampling has occurred (source: Menez, 2001).



Tattersfield, 1990, 1998; Emberton *et al.*, 1996; Wardhaugh, 1996; Chater, 1998; Ramos, 1998; Cameron *et al.*, 2007; Čejka *et al.*, 2008, and Table 3.4.) including those undertaken in Iberia (Altonaga, 1988; Puente, 1994; Arrébola, 1995; Martinez-Orti, 1999). The method is also used for collecting slugs

(Hunter, 1968), although numbers tend to be underestimated because aspects of behaviour, including burial into soil during parts of the year (Quick, 1960; Newell, 1968; Wäreborn, 1969; Runham and Hunter, 1970; Kerney and Cameron, 1979), result in slugs being more difficult to find than snails. In the Mediterranean region slugs are sometimes found only during the wet period (unpublished data; Cameron *et al.*, 2003).

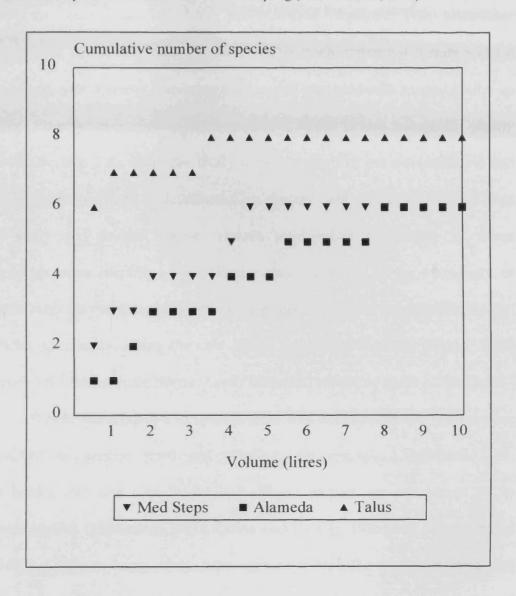
Each site in the present study was searched for 2.5 hours. This has been shown to be adequate for sampling Mediterranean habitat types (Menez, 2001 and Figure 3.4.) and approximates to time periods used in other recent studies (Cameron et al., 2000, 2003). At all sites a thorough searching of plants, under rocks and logs and other types of habitat structure, was carried out. This is similar to other studies for land molluscs (see references above) and the method's efficacy at finding land molluscs depends, to varying degrees, on the experience of the fieldworker to sample a site adequately (Ward-Booth and Dussart, 2001). In studies that use more than one worker this has sometimes proved problematic because of the differential capacity of workers to sample sites and, if these workers sample different sites that are then compared, collector bias may be a concern. This is not a problem in this study, however, because all sampling was carried out by only one worker (the author) and any collector bias is assumed to be standardized across all sites.

3.5.2. Collection of specimens from soil

At each site a total of five litres of soil were collected from five randomly selected points (1 litre at each point). One litre of soil was collected at each of the points corresponding to 30, 60, 90, 120 and 150 minutes of the 2.5 hours direct search period. It is accepted, however, that more species may have been

recorded if soil had been collected at points identified a priori as being likely to contain more molluscs (such as at the base of rocks and under logs). This volume of soil has been shown to be adequate for sampling the molluscs in soil in Mediterranean habitat types (Menez, 2001 and Figure 3.5.). The soil was pooled and then dried in a hot air oven at 90°C for 18 hours and allowed to cool to 20°C. This process removes moisture and allows efficient sieving of the soil. The soil was sieved using 6mm and 1mm mesh sieves in a hand held frame that separates the soil into three fractions. The 6mm and 1mm fractions were examined for molluscs using a 6x magnifying lens, and the <1mm fraction was examined using 20x magnification with a stereo dissecting microscope. A limitation is that the method kills molluscs in the soil resulting in some species, especially slugs, being difficult or impossible to identify. An improvement would be to use soil washing and flooding techniques to extract live molluscs from the soil, prior to heating (Runham and Hunter, 1970; Pearce and Örstan, 2006).

Figure 3.5. The species-volume (of soil) relationships for three sites representing three Mediterranean habitat types: Med Steps=maquis; Alameda=man-induced (gardens); Talus=coastal (sand). At each site ten litres of soil were collected from a randomly selected point and thoroughly mixed and then divided into 20 0.5litre aliquots. Samples were sieved through 6mm and 1mm sieves and the fractions examined under magnification for land molluscs (see text for details). The mean volume at which asymptotes are attained is 4.2 litres, indicating this to be an adequate volume of soil to use for sampling (source: Menez, 2001).



3.6. Identification of the species

Most of the specimens were identified to species level, and material from the author's extensive collection of southern Iberian land molluscs was used for comparison. Published, and unpublished, literature was used to verify the genital anatomy of those specimens that required dissection for identification

(e.g. Puente, 1994; Arrébola, 1995; Martinez-Orti, 1999). Most of these were from the genera Xerosecta, Iberus and Theba, but also from other genera including Trochoidea and Candidula which contain smaller species. Many specimens were identified from conchological features. This sometimes required the use of magnification to examine micro-structural details and for these specimens a stereo dissecting microscope was used with magnification up to 20x. From an area such as southern Iberia, which is malacologically poorly known (Section 1.4), there are likely to be species that are unidentifiable and which may be presently undescribed. This was the case with some material from this study and several species remain unidentified (Appendix 3). Some specimens were identified by Professor José Arrébola of the University of Seville who also prepared dissection diagrams to assist in the identification of difficult species, including the rare Theba subdentata helicella (Wood, 1828) (Figure 3.6.). Mr. Adrian Norris (Leeds Museum) identified some of the slugs.

Where identification to species level was not possible the species were identified to generic level and labelled, for example, *Trochoidea* sp1, *Trochoidea* sp2 and *Trochoidea* sp3. These species are considered to be morphospecies (Hammond, 1994; Oliver and Beattie, 1996) and were matched conchologically as being of the same species at both the same site (intra-site) and across sites (inter-site) where they occurred. All specimens are catalogued and kept in the author's collection, which in the future will be lodged in the Gibraltar Museum.

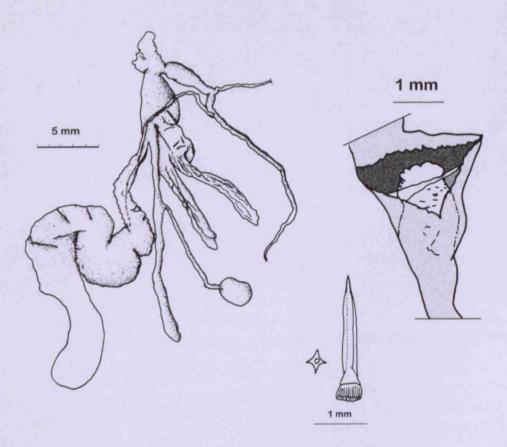
Figure 3.6. Theba subdentata helicella (Wood, 1828) from Retamar, Spain. a. shells (scale in mm) b. dissection carried out by author (scale in mm) c. diagram of genitalia, internal structure of penis and dart from confirmatory dissection (diagram c. courtesy of José Arrébola, University of Seville).



a



b



C

3.7. Data analysis

3.7.1. Diversity analysis

3.7.1.1. The number of species

Also known as species richness (McIntosh, 1967) this is a measure of the number of species at each of the sites. It is the oldest measure of biological diversity (MacArthur, 1965; Magurran, 2004) but as purely a measure of number of species, there is generally no implied standardization of sampling. Species density is the number of species in a standardized sample (e.g. per unit area) and is a rarely used measure (Whittaker *et al.*, 2001).

3.7.1.2. Abundances of the species

The numbers of individuals of each of the species at each of the sites were recorded to provide the abundance of each species. The term abundance is synonymous with density when (as in this study) the unit of area or volume from which the species are counted, is known (Krebs, 1985; Bullock, 1996).

3.7.1.3. Diversity

There is considerable controversy and debate about how species diversity should be measured and some indices make assumptions that are sometimes not met by the species data that they are used for (see Magurran, 2004, for discussion). A large body of literature exists and the following provide details and discussion about these debates: McIntosh, 1967, 1985; Hurlbert, 1971; Connell, 1978; Green and Vascotto, 1978; Southwood, 1978; Huston, 1979; Yapp, 1979; Wolda, 1983; Gadagkar, 1989; Lande *et al.*, 2000; Keylock, 2005, with Magurran (2004) providing a recent synthesis of the species diversity measurement debate as well as discussion about new measures including Clarke and Warwick's taxonomic distinctness index (see also Warwick and Clarke,

1995; 1998; Ellingsen et al., 2005; Salas et al., 2006). In this study two indices of species diversity were used: Simpson's index (Ds), and the Shannon index (H') (Magurran, 1988, 2004; Keylock, 2005). These two indices are commonly used in ecological studies, their efficacy and robustness are well known (Magurran, 2004), and they allow comparisons of the data from this study with other studies (Section 8.2).

Although diversity indices have limitations, related to sample size and species evenness, their advantage in assessing community composition and related ecological relationships is that a significant amount of data can be summarized by one value, or set of values (Hurlbert, 1971; Magurran, 2004).

McCoy (1999) used the Shannon index to measure the diversity of land molluscs indicating that this choice had been made because the index makes no assumptions about the shape of the underlying distribution of species abundance and is relatively insensitive to changes in the dominant species. Lande et al. (2000) demonstrated that Simpson's index always produces a consistent expected ranking among communities across sample size, even at low sample sizes. They also showed that 81 individuals were sufficient to rank Simpson's diversity within 95% confidence intervals, whereas 1801 individuals were required to rank species richness using species accumulation curves. They further pointed out that intersection of accumulation curves for two communities will occur if one community contains a greater number of species but has lower evenness, and thus a lower value for Simpson's index. Curves tend to intersect when comparing communities that differ in habitat heterogeneity and/or disturbance regimes. Lande et al. (2000) also state that of the diversity indices, only Simpson's has the statistical accuracy for reliable

comparisons among communities using small samples, and that because the estimator of Simpson's index is unbiased, it is statistically valid to compare Simpson's index in communities with different sample sizes.

3.7.1.3.1. Simpson's index

This is calculated using $D = \frac{\sum n_i(n_i - 1)}{N(N - 1)}$ where n_i is the number of individuals of the *i*th species and N is the total number of individuals. The reciprocal form (Ds) is used to ensure that the value of the index increases with increasing diversity; this is given by $Ds = \frac{1}{D} = \frac{N(N-1)}{\sum n_i(n_i - 1)}$ (Magurran, 2004).

3.7.1.3.2. Shannon index

This is calculated using $H' = -\Sigma p_i \ln p_i$ where p_i , the proportional abundance of the *i*th species = (n_i/N) . Base 2 logs were used for calculating the Shannon index (Magurran, 2004). The indices were derived from the species abundances matrix using the DIVERSE routine in PRIMER (Plymouth Routines in Multivariate Ecological Research; Carr, 1991, 1997; Clarke and Warwick, 1994).

To assess all of the measures described in Sections 3.7.1.1 to 3.7.1.3 the mean, 95% confidence intervals (CI), minimum, maximum and range were used. CI were used instead of standard error (SE) of the mean following Dytham (2003) who states that CI is preferred over SE because the latter is useful only if the sample size is known. This criterion is almost never met with number of species and species abundances data.

The observed sample mean (x) and its standard error (s.e.= s/\sqrt{n}) are used to estimate a range within which the population mean is likely to lie. There is a 95% probability that the sample mean lies with 1.96 s.e. below or above the population mean and therefore a 95% probability that the interval between x-1.9

s.e. and x+1.96 s.e. contains the (unknown) population mean. The 95% confidence interval (CI) is given by: 95% CI = $x\pm(1.96xs/\sqrt{n})$ (Kirkwood, 1988; Dytham, 2003).

3.7.2. Biogeographical analysis

3.7.2.1. Classification (Cluster)

This technique is widely used in ecological studies to classify sites, species or variables, giving information on which species are found together, establishing community types and determining relationships between communities and environmental variables by analyzing clusters (Tongeren, 1995). A group average hierarchical agglomerative method was carried out using the CLUSTER routine in PRIMER. This is the cluster method that is the most used in ecological studies. Samples from a similarity matrix (using the Bray-Curtis similarity coefficient) are agglomerated into groups, and the groups into larger clusters, beginning with the highest mutual similarities and then gradually lowering the similarities during group formation with each new node taking the average similarity of the individual nodes rather than the minimum (for complete linkage) or maximum (for single linkage) similarities.

Cluster analysis was carried out on (1) the samples (i.e. sites) using the \log_{x+1} transformed species abundances to identify site groupings and, (2) on the standardized species abundances to assess species similarities. The second approach defines the similarity between any pair of species (in an analogous way to that for the samples), but is done by comparing the *i*th and *l*th row (species) across all columns (i.e. samples; see Section 4.2.2 for details).

3.7.2.2. Ordination (MDS)

Ordination techniques have been widely used in ecology since Principal Components Analysis was first used by Goodall in the early 1950s for classifying vegetation (Goodall, 1954; Zitko, 1994). Of the many techniques that are now available, Non-Metric Multidimensional Scaling (MDS) is one of the most used, and the one used in this study. The procedure uses the similarity matrix (using the Bray-Curtis similarity coefficient) to construct a configuration, or map, of the samples such that samples that are more similar are closer together. MDS uses an iterative algorithm to obtain the best configuration of points (samples), assessed using the stress function calculated for each configuration. The results of cluster and MDS often complement one another and both techniques are often used together in studies (Carr, 1991, 1997; Clarke and Warwick, 1994). MDS was carried out using the MDS routine in PRIMER.

3.7.2.3. Linking environmental variables to species data (BIOENV)

An overview of this method is given here because as far as the author is aware this study is the first that uses the BIOENV method with land molluscs. Many techniques have been used in ecology to find and explain species' distribution patterns (Clifford and Stephenson, 1975; Field et al., 1982; Clarke and Ainsworth, 1993). These techniques can be classified into three main groups: (1) a search for patterns amongst the species data with an attempt to interpret these in terms of the environmental data, (2) a search for patterns of relationships between the species data and environmental data simultaneously, and (3) a search for patterns amongst the environmental data followed by a search for related patterns in the species data. The third approach is recommended by Green and Vascotto (1978) and Field et al. (1982) because the

influence of any previous assumptions about relationships between the species and environmental data are avoided.

These approaches only permit one environmental variable at a time to be related to the species data ordination (Clarke and Ainsworth, 1993; Freeman and Rogers, 2003). This has led to the development of a technique that uses the rank similarity matrices of ordination methods of environmental and species data to define an optimal subset of environmental variables that best explain the species data (Clarke, 1993; Clarke and Ainswoth, 1993). The among-sample similarity matrix for the species data was constructed once using MDS (Section 3.7.2.2), but the equivalent triangular matrix for the environmental data was computed for all possible combinations of environmental variables at each level of complexity of explanation (i.e. variables taken singly, two at a time, three at a time etc.) using Principal Components Analysis.

The rank correlations between the species and environmental matrices were calculated in every case. A down-weighting to Spearman's rank correlation coefficient is applied that permits a better understanding of the coefficient's behaviour (Clarke and Ainsworth, 1993). This down-weighting is achieved by adding a denominator term inside the summation that is an increasing (and symmetric) function of r_i and s_i where $\{r_i; i=1,...,N\}$ are the number of all the sample similarities calculated using the species data and $\{s_i; i=1,...,N\}$ are the ranks of sample similarities defined from the environmental data. The weighting term is $(r_i + s_i)$ giving the weighted coefficient p_w . This has been termed the Harmonic rank correlation by Clarke and Ainsworth (1993) and:

 $p_w = 1 - c \sum_{i=1}^{N} \frac{(r_i - s_i)^2}{(r_i - s_i)}$ where p_w ranges from 0 to 1. A value of 0 denotes no

correlation and a value of 1 denotes complete correlation. The highest value of p_w from the analysis is chosen and represents the best explanation of the species data by the environmental data. A limitation of the method is that there is no testing framework that can assess the statistical significance of the optimal combination of species and environmental variables, and the value of p_w is used alone (Clarke and Ainsworth, 1993; Clarke and Warwick, 1994).

Computations were carried out using the BIOENV routine in PRIMER.

3.7.2.4. Commonness and Rarity

In this study commonness and rarity are considered in relation to the total abundance of each species at all sites (Gaston, 1994; Kelly *et al.*, 2001). The species were ranked according to their total abundances (most abundant to least abundant, starting at rank 1) and assessed in relation to distribution in the entire study area (Section 3.7.2.5).

3.7.2.5. Species distributions

Species were assigned to one of three distributional ranges: Mediterranean (present only in the range represented by Sites 1 to 48), Atlantic (present only in the range represented by Sites 49 to 91) and, Mediterranean-Atlantic (present in the range represented by all sites). In addition, species were assigned as having narrow distributions if they were present only at Mediterranean, or only at Atlantic, sites, and as having wide distributions if found at both Mediterranean and Atlantic sites. These classifications can only serve as a preliminary guide to the distributions of these species and more fieldwork is required to determine distributional ranges more accurately.

3.7.2.6. Numbers of species per family

The number of species in each family was quantified using data from each of their distributional ranges (Section 3.7.2.5). This was then calculated as a percentage.

3.7.2.7. Species abundance models

Fisher et al. (1943) showed that a characteristic pattern of species abundance was present in data sets, which led to the development of species abundance models (Magurran, 1988). A species abundance distribution uses all the information from a sampled point and is the most complete mathematical description of the data (Magurran, 1988). Many workers (see for example May, 1975, 1981; Southwood, 1978) suggest these provide the only sound basis for the analysis of species diversity.

Many models have been proposed (Pielou, 1979; McIntosh, 1985; Magurran, 1988) but data are usually examined with one or more of these main models: (1) geometric series, (2) log series, (3) log normal, (4) truncated log normal, and (5) broken stick. In some cases more than one model describes a data set (e.g.: Thomas and Shattock, 1986; Menez, 1996, and this study).

The geometric and log series are closely related (May, 1975) and generally indicate strong dominance in 'harsh' environments or in early stages of succession (He and Tang, 2008). The log normal indicates a sequential splitting of the community multidimensional niche space (Sugihara, 1980) and may fit data from large, diverse communities. The truncated log normal is related to the log normal. In finite samples the left hand part of the curve is obscured and the truncation point is further from the origin in smaller samples. The model predicts the total number of species in the community (S^*). The

broken stick indicates high equitability and is mostly found in narrowly defined communities of taxonomically-related organisms (Magurran, 1988).

The curves for these models are generally fitted visually, and have rarely been mathematically-fitted to data (Wilson, 1991). In this study the species abundances data from each site were tested for mathematical fit to these five models using a BASIC program based on formulae from Magurran (1988). The models that best fitted each data set were selected using the *P* values derived by the program. These models are used to describe the species abundances data from rank/abundance (also termed Whittaker or dominance/diversity) curves. Data analyses of this type have become popular in the ecological literature in recent years (Watkins and Wilson, 1993; Krebs, 1999; Magurran, 2004) and Magurran (2004) reports that standardization of plotting methods may soon be achieved.

3.7.2.8. Beta diversity (β)

Beta diversity is a measure of the change in diversity between samples and was first used by Whittaker (1960) for samples across environmental gradients or along transects. The measure can also be used to assess change in diversity between different sites or locations, and to assess diversity over time (Magurran, 2004). Temporal and spatial changes in diversity are commonly called *turnover* (Huston, 1994; Magurran, 2004; Begon *et al.*, 2006). In this study, Whittaker's measure of Beta diversity (β_w) was used (Whittaker, 1960, 1970) to measure the between-sites diversity. This is calculated using $\beta_w = S/\alpha$ where S is the total number of species recorded at a site, and α is the mean sample diversity.

3.7.2.9. Transformations

Transformations were carried out on data for two different reasons (Clarke and Warwick, 1994; Sokal and Rohlf, 1995):

- 1. to validate the assumptions for parametric tests;
- 2. to weight the contributions of common and rare species in multivariate analyses.

Data were analyzed using the Kolmogorov-Smirnov test (K-S) for goodness of fit using the one sample K-S routine in SPSS (Statistical Package for the Social Sciences, Norusis, 1986) that compares the data with a theoretical normal distribution and computes K-S z. If the distribution of the data is significantly different from normal the significance (2-tailed P) is less than 0.05.

A variety of transformations can be used ranging from a square root transformation to converting the data to presence/absence. This range can be considered to be a sequence, which corresponds to a progressive downweighting of the common species, and is (from Clarke and Warwick, 1994; Legendre and Gallagher, 2001):

None
$$\rightarrow \sqrt{x} \rightarrow \sqrt{x}$$
 or $\log_{x+1} \rightarrow$ presence/absence

The choice is between a moderate $(\sqrt{})$ and fairly severe $(\sqrt{}\sqrt{})$ or log) transformation and converting the data to presence/absence format. The $\sqrt{}\sqrt{}$ or \log_{x+1} transformation is generally recommended because it retains quantitative information from the species abundances yet still downplays the species dominants. In this study the \log_{x+1} transformation is used for both species and environmental data.

3.7.3. Local and regional scales

Community ecology has long been considered to be the result of local environmental and ecological processes such as competition and predation (Kikkawa and Anderson, 1986; Ricklefs, 1987). Local processes, however, may be insufficient to provide explanations for the local co-existence of species (Shimda and Wilson, 1985; Lawton, 1999), and the relative impact of local and regional processes on community structure partly depends on the intensity of interactions at the local scale (Cornell and Lawton, 1992; Niemelä *et al.*, 1996; Mouquet *et al.*, 2001). More recently, the influence of local processes has been complemented by the recognition of other environmental factors that generate non-random patterns of community composition, and which are termed regional factors (Ricklefs and Schluter, 1993; Gaston, 2000; Whittaker *et al.*, 2001).

Local richness is measured on a scale small enough that all species could encounter each other (and possibly interact) within ecological time. Regional richness is the species pool and contains all species that could eventually colonise a location if competitive exclusion was unimportant (Griffiths, 1999; Srivastava, 1999). The term landscape is often used to denote a scale between local and regional scales (Forman and Godron, 1986; Forman, 1995; McGarigal and McComb, 1995; Irmler and Hoernes, 2003).

In general, alpha diversity corresponds to the local scale, beta diversity to the landscape scale and gamma diversity to the regional scale, although these are related to the body sizes of taxa, and the scales at which alpha, beta and gamma diversities are applicable vary between taxa (Emberton, 1995a; Whittaker *et al.*, 2001). Nekola and Smith (1999), for example, report that their results for Wisconsin carbonate cliff land mollusc communities suggest that

alpha diversity at these sites is best measured at scales no larger than 0.04m², beta diversity at scales no larger that 100m², and gamma diversity is best measured between sites at least 10km distant from one another.

Many land mollusc studies differentiate between local and regional scales in assessment of diversity (e.g. Tattersfield, 1996; Nekola and Smith, 1999; Cameron et al., 2000) and in this study local scale refers to sites, and regional scale to the entire study area (sensu Casado et al., 2004; Gray et al., 2005).

CHAPTER 4. RESULTS AND DISCUSSION

4.1. Diversity analysis: results

4.1.1. The numbers of species, abundances and diversity

A total of 94 species were recorded from the 91 sites (Table 4.1; see Appendix 3 for systematic species list, Appendix 4 for species abundances at the sites).

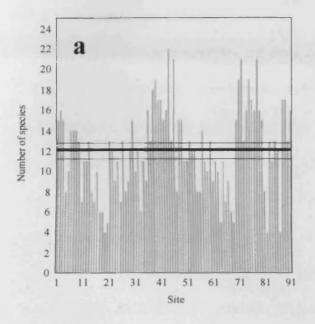
Table 4.1. The number of species, total abundances, Shannon diversity and Simpson's diversity at the 91 sites. Lower 95% CI and upper 95% CI are lower and upper 95% confidence intervals of the mean, respectively.

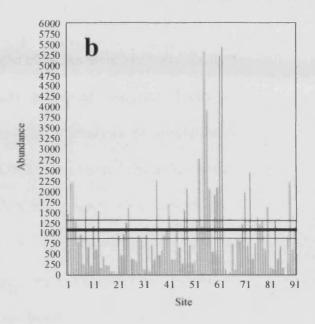
Variable	Mean	Minimum	Maximum	Range	Lower 95% CI	Upper 95% CI
Number of species	12.1	4	22	18	11.2	13.0
Total abundance	1068.8	6	5450	5444	843.8	1293.7
Shannon diversity	2.380	0.452	3.717	3.266	2.253	2.507
Simpson's diversity	0.724	0.130	0.933	0.803	0.694	0.754

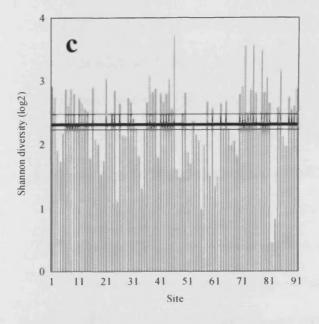
There were two areas with greater numbers of species and diversities than others (Figure 4.1.a,c,d): the Mediterranean coast from Benagalbon (Site B36) to Sotogrande (Site B46), and the Atlantic coast from Tavira (Site B70) to São Vicente (Site B81). The species *Cochlicella acuta* (Müller, 1774) is very abundant in southern Iberia and four sites had total abundances greater than 3000 (Figure 4.1.b.) attributable to the high abundances of this species (Appendices 3 and 4).

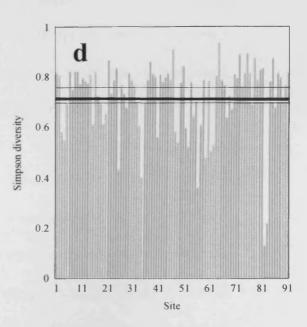
Nonparametric species estimators, such as Chao 1 and Chao 2, are efficient at estimating the number of species in samples (Magurran, 2004). The estimators, however, assume homogeneity amongst the samples (Magurran, 2004) and cannot be used with the data from Part One as sites were not all of the same habitat type.

Figure 4.1. The numbers of species (a), total abundance (b), Shannon diversity (c) and Simpson's diversity (d) for the 91 sites. In each graph the mean (bold line) and lower and upper 95% confidence intervals of the mean (fine lines) for the data are shown. See Appendix 1 for site details.









4.2. Biogeographical analysis: results

4.2.1. The environmental variables

Values for the environmental variables for each site are listed in Appendix 5.

4.2.2. Classification (Cluster)

The data for the cluster analyses are from single sites. As there are no replicates at sites it has not been possible to undertake statistical analyses of cluster memberships; hence the permutation test ANOSIM (analysis of similarities) available in PRIMER has not been used. ANOSIM tests the null hypothesis that there are no differences in community composition at sites using permutation and randomization methods on the within- and between-sites species similarities. Non-replication at sites also prevents the use of SIMPER (similarity percentages), available in PRIMER, which computes the contribution of each species to the mean dissimilarity both within and between groups (Clarke and Warwick, 1994). A study such as this could be improved by sampling with replication at sites to allow statistical analyses of species similarities using methods such as ANOSIM and SIMPER. Although this has not yet been done using land molluscs at the biogeographical scale considered here (because of time constraints resulting from the number of replicates needed), it merits consideration for future studies (Section 8.5).

The groups in the cluster analyses were assessed at two different similarity thresholds. A threshold of 50% was used for the analysis to cluster all 91 sites based on their species compositions (samples analysis), and a threshold of 20% for the analyses of species similarities from all sites. The assignment of threshold values to assess group membership is largely arbitrary and it is customary to use values of 50% or more (Clarke and Warwick, 1994; Tongeren,

1995). In the present study similarity was low for the species similarity analyses and a cut-off value of 20% was required to differentiate main groups.

4.2.2.1. Samples analysis

Clustering of the \log_{x+1} species abundances from the sites formed 34 groups (Figure 4.2 and Table 4.2). Group 34 contained 16 sites (17.6 % of the total) and the remaining sites were in groups containing between one and seven sites (Table 4.2); of these groups, 16 (48% of the total) contained only one site. Group 34 contains most of the sites located on the east coast from Malaga, Spain, to Portimão, Portugal. Group 30 contains sites from the east coast from San Pedro de Alcantara, Spain, to Sotogrande, Spain. Some of these sites have the highest diversities recorded from the study area and this group includes the site with the highest diversity (Sotogrande, H'=3.717, Appendix 1).

The low levels of similarity between most sites indicate that there is a low level of similarity between the land mollusc communities. These results are supported by the fact that 89 of 91 sites formed single-site groups at a level of similarity of 80% (89 sites =98% of the total, Figure 4.2, Section 4.2.2.2). Using species presence/absence for cluster analysis results in similar groupings of sites to the \log_{x+1} transformed species abundances.

Plotting the Bray-Curtis similarity coefficient for each of the sites, arranged in sequential order from Guardamar del Segura, Spain (Site B1) to Lagoa de Santo André, Portugal (Site B91), illustrates the decrease in similarity between sites moving across sites from B1 to B91. This represents an increase in distance away from Site B1 of about 10-15km from one site to the next, over the approximately 1500km extent of the study area (Section 3.2). This decrease in similarity is highly significant (r_s =-0.632, P<0.001, Figure 4.3).

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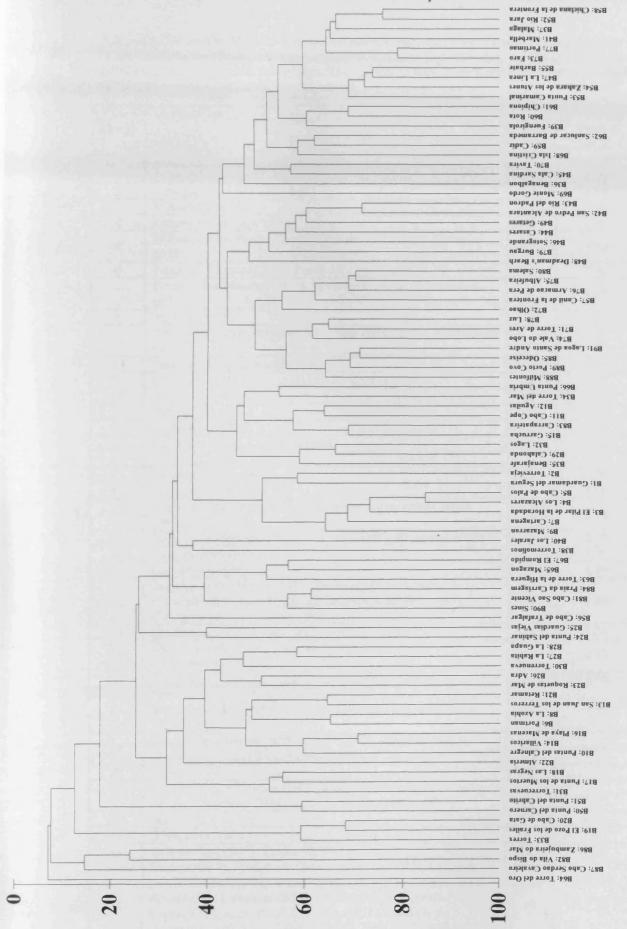


Figure 4.2. Dendogram of all species from the sites (log_{v+1} species abundances). Sites are on the x axis and Bray-Curtis similarity coefficients on the y axis.

Table 4.2. The results of group average hierarchical agglomerative clustering (using the Bray-Curtis similarity coefficient) on \log_{x+1} species abundances from the sites. A 50% similarity cutoff is used for site inclusion into groups. The number of sites in each group, and the percentage of the total sites this represents, are also shown.

Group	Sites in Group	No. of sites	Percentage of total sites (n=91)
1	Torre del Oro (B64)	- 1	1.09
2	Cabo Serdão Cavaleiro (B87)	1	1.09
3	Vila do Bispo (B82)	1	1.09
4	Zambujeira do Mar (B86)	1	1.09
5	El Pozo de los Frailes (B19), Cabo de Gata (B20), Torrex (B33)	3	3.30
6	Punta del Carnero (B50), Punta del Cabrito (B51)	2	2.20
7	Punta de los Muertos (B17), Las Negras (B18), Torrecuevas (B31)	3	3.30
8	Almeria (B22)	1	1.09
9	Puntas del Calnegre (B10), Villaricos (B14), Playa de Macenas (B16)	3	3.30
10	Portman (B6), La Azohia (B8)	2	2.20
11	San Juan de los Terreros (B13), Retamar (B21)	2	2.20
12	Roquetas de Mar (B23)	1	1.09
13	Adra (B26)	1	1.09
14	Torrenueva (B30)	1	1.09
15	La Rabita (B27), La Guapa (B28)	2	2.20
16	Punta del Sabinar (B24)	1	1.09
17	Guardias Viejas (B25)	1	1.09
18	Cabo de Trafalgar (B56)	1	1.09
19	Cabo São Vicente (B81), Praia da Carriagem (B84), Sines (B90)	3	3.30
20	Torre de la Higuera (B63), Mazagon (B65), El Rompido (B67)	3	3.30
21	Torremolinos (B38)	1	1.09
22	Los Jarales (B40)	1	1.09
23	Guardamar del Segura (B1), Torrevieja (B2), El Pilar de la Horadada (B3), Los Alcázares (B4), Cabo de Palos (B5), Cartagena (B7), Mazarrón (B9)	7	7.69
24	Calahonda (B29), Lagos (B32), Benajarafe (B35)	3	3.30
25	Cabo Cope (B11), Aguilas (B12), Garrucha (B15), Carrapateira (B83)	4	4.40
26	Torre del Mar (B34), Punta Umbria (B66)	2	2.20
27	Torre de Ares (B71), Vale do Lobo (B74), Luz (B78), Odeceixe (B85), Milfontes (B88), Porto Covo (B89), Lagoa de Santo André (B91)	7	7.69
28	Conil de la Frontera (B57), Olhão (B72), Albufeira (B75), Armação de Pera (B76), Salema (B80)	5	5.49
29	Deadman's Beach (B48)	1	1.09
30	San Pedro de Alcantara (B42), Rio del Padrón (B43), Casares (B44), Sotogrande (B46), Getares (B49), Burgau (B79)	6	6.59
31	Monte Gordo (B69)	-1	1.09
32	Benagalbon (B36)	1	1.09
33	Cala Sardina (B45), Tavira (B70)	2	2.20
34	Malaga (B37), Fuengirola (B39), Marbella (B41), La Línea (B47), Rio Jara (B52), Punta Camarinal (B53), Zahara de los Atunes (B54), Barbate (B55), Chiclana de la Frontera (B58), Cadiz (B59), Rota (B60), Chipiona (B61), Sanlúcar de Barrameda (B62), Isla Cristina (B68), Faro (B73), Portimão (B77)	16	17.58
	(B77) Σ	91	99.88

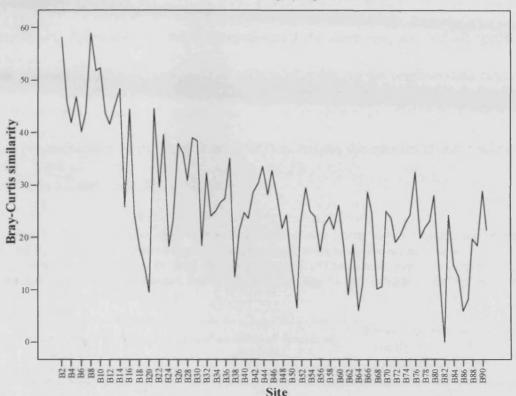


Figure 4.3. The Bray-Curtis similarity coefficient for each of the sites, arranged in sequential order from Site B1 (Guardamar del Segura, Spain) to B91 (Lagoa de Santo André, Portugal). The decrease in similarity from Site B1 to B91 is highly significant (r_s =-0.632, P<0.001).

4.2.2.2. Species similarities

Cluster analyses to identify species similarities (Section 3.7.2.1) were carried out on standardized, and not transformed, species abundances (Clarke and Warwick, 1994). Standardizing in this way provides the percentage of total abundance (over all species) that is accounted for by each species. Each matrix entry is divided by its column total and multiplied by 100 to form the new array of values. Clarke and Warwick (1994) recommend the removal of the rarer species from the matrix before similarities are assessed. If this is not done cluster analysis may fail to provide an interpretable result. The methods used to reduce the matrix are arbitrary, but Field *et al.* (1982) suggest the removal of all species that never constitute more than p% of the total abundance of any sample, where p is chosen to retain approximately 50 or 60 species in large matrices. In most cases p is generally about 3%.

This method is generally not used for *between-sample* similarity calculations (Section 4.2.2.1). In these cases the calculation of the Bray-Curtis coefficient down-weights the contributions of the rarer species, and all species are retained in the calculations. The effects of reducing the original data matrix of 94 species by different percentage values (*p*, above) are given in Table 4.3. The recommendation of Field *et al.* (1982) to reduce the species at the 3% level results in 62 species in the analysis.

Table 4.3. The percent level used to reduce the species data matrix before cluster analysis was carried out, showing number of species at each percent level and the number of species used in cluster analysis as a percent of total species at all sites. (*The species matrix was reduced by removing species that constituted less than this percentage of any sample). Shading indicates levels assessed in the present study.

Percent level used to reduce matrix *	Total number of species in analysis	Total number of species in analysis as % of total species at all sites
3	62	66.0
5	59	62.8
10	48	51.1
15	40	42.6
20	36	38.3
25	31	33.0

Clustering at the 3% level formed 30 groups (Figure 4.4, Table 4.4). Of these, 14 groups (45.2%) were represented by only one species, and 13 groups (41.9%) by two to three species. These findings indicate that there is low similarity between species, even when the rarer species have been excluded from the analyses (Section 4.2.2.1). The three groups that contain five or six species provide the only clearly interpretable species associations.

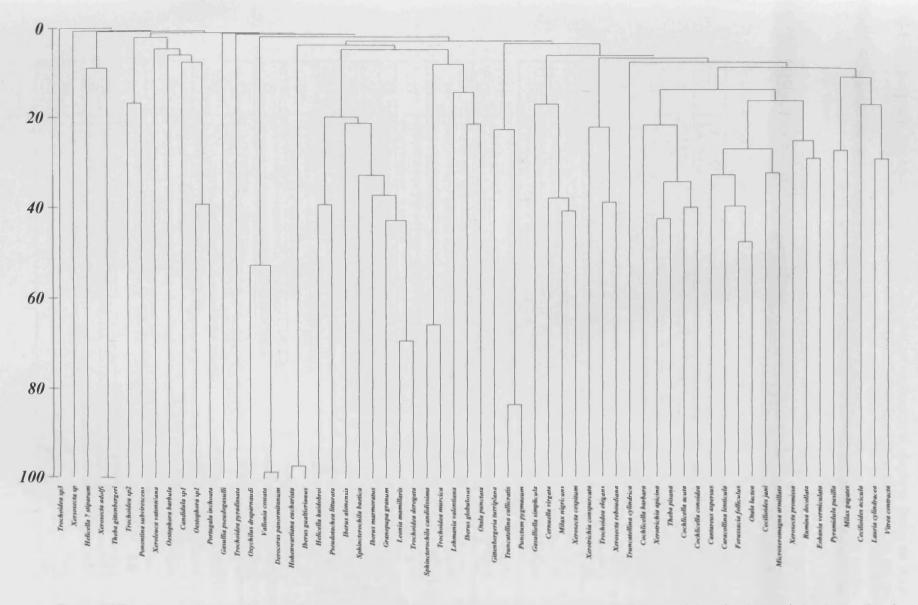


Figure 4.4. Dendogram of species from the sites (standardized species abundances). The species used are those remaining after the matrix has been reduced by removing species that constitute less than 3% of any sample. Species are on the x axis and Bray-Curtis similarity coefficients on the y axis.

Table 4.4. The results of group average hierarchical agglomerative clustering (using the Bray-Curtis similarity coefficient) on standardized species abundances from the sites. The species used are those remaining after the matrix has been reduced by removing species that constitute less than 3% of any sample. A 20% similarity cut-off is used for species inclusion into groups. The number of species in each group, and the percentage of the total species this represents, are also shown.

Group	Species in Group	Number of species	Percentage of total species (n=62)	
1	Trochoidea sp3	1	1.61	
2	Xerosecta sp	-1	1.61	
3	Helicella? stiparum	1	1.61	
4	Xerosecta (Xerosecta) adolfi, Theba gittenbergeri	2	3.23	
5	Trochoidea sp2	1	1.61	
6	Ponentina subvirescens	1	1.61	
7	Xeroleuca vatonniana	1	1.61	
8	Oestophora barbula	1	1.61	
9	Candidula sp1	1	1.61	
10	Oestophora sp1, Portugala inchoata	2	3.23	
11	Hatumia pseudogasulli	1	1.61	
12	Trochoidea (Trochoidea) pyradimata	1	1.61	
13	Oxychilus (Oxychilus) draparnaudi, Vallonia costata, Deroceras (Deroceras) panormitanum	3	4.84	
14	Hohenwartiana eucharista, Iberus gualtierianus gualtierianus	2	3.23	
15	Helicella huidobroi, Pseudotachea litturata,	2	3.23	
16	Iberus gualtierianus alonensis, Sphincterochila (Cariosula) baetica, Iberus gualtierianus marmoratus, Granopupa granum	6	9.68	
17	Sphincterochila (Albea) candidissima, Trochoidea (Xerocrassa) murcica	2	3.23	
18	Lehmania valentiana	1	1.61	
19	Iberus gualtierianus globulosus, Otala (Otala) punctata	2	3.23	
20	Gittenbergeria turriplana, Truncatellina callicratis, Punctum (Punctum) pygmaeum	3	4.84	
21	Gasulliella simplicula	1	1.61	
22	Cernuella (Cernuella) virgata, Milax nigricans, Xerosecta (Xerosecta) cespitum	3	4.84	
23	Xerotrichia conspurcata, Trochoidea (Trochoidea) elegans, Xerosecta (Xerosecta) reboudiana	3	4.84	
24	Truncatellina cylindrica	1	1.61	
25	Cochlicella (Prietocella) barbara, Xerotrichia apicina, Theba pisana, Cochlicella (Cochlicella) acuta, Cochlicella (Cochlicella) conoidea	5	8.06	
26	Cantareus aspersus, Caracollina (Caracollina) lenticula, Ferussacia (Ferussacia) folliculus, Otala (Otala) lactea, Cecilioides (Cecilioides) jani, Microxeromagna armillata	6	9.68	
27	Xerosecta (Xerosecta) promissa, Rumina decollata, Eobania vermiculata	3	4.84	
28	Pyramidula pusilla, Milax gagates	2	3.23	
29	Cecilioides (Cecilioides) acicula	1	1.61	
30	Lauria (Lauria) cylindracea, Vitrea (Crystallus) contracta	2	3.23	
	Σ	62	100	

Group 16 (Table 4.4) contains species that are present at many of the sites on the east coast (e.g. *Granopupa granum* (Draparnaud, 1801)), or that occur *only* at these sites (*Sphincterochila (Cariosula) baetica* (Rossmässler, 1854)). Group 25 contains species that are frequently present together at sites with sandy soils (e.g. *Theba pisana* (Müller, 1774) and *C. acuta*), and Group 26 contains species that are wide-ranging across the study area (Appendix 3), present at a large number of sites, and very abundant (Table 4.9) (e.g. *Caracollina (Caracollina) lenticula* (Michaud, 1831) and *Ferussacia (Ferussacia) folliculus* (Gmelin, 1790)). Species from Groups 25 and 26 are among the most abundant of all species from the study area (Table 4.9).

The reduction of the species matrix to the 25% level supports the findings of analysis at the 3% level. The number of groups formed changes from 30 (with 3% reduction) to 14 (Figure 4.5 and Table 4.5). Even at this level of reduction there are still 11 (78.6%) groups with only one or two species. This is further evidence that there exists low similarity between species, and adds to the evidence showing this from the sample-similarity analysis (Figure 4.2, Table 4.2). The three clearly interpretable groups provide results similar to those of the 3% reduction analysis. Although there are some differences in memberships of these three groups using the two levels of reduction, they arguably indicate the same thing (Table 4.6).

Overall, the results indicate an extremely low level of species similarity in the southern Iberian malacofauna. There are endemics, rare species and species with reduced ranges (e.g. *Hohenwartiana eucharista* (Bourguignat, 1864), *Helicella ? stiparum* (Rossmässler, 1854) and *Xeroleuca vatonniana*

(Bourguignat, 1867)) but these mostly form groups with single-species membership.

Table 4.5. The results of group average hierarchical agglomerative clustering (using the Bray-Curtis similarity coefficient) on standardized species abundances from the sites. The species used are those remaining after the matrix has been reduced by removing species that constitute less than 25% of any sample. A 20% similarity cut-off is used for species inclusion into groups. The number of species in each group, and the percentage of the total species this represents, are also shown.

Group	Species in Group	Number of species	Percentage of total species (n=31)
1	Trochoidea sp2	1	3.23
2	Ponentina subvirescens	1	3.23
3	Portugala inchoata	1	3.23
4	Lauria (Lauria) cylindracea, Vitrea (Crystallus) contracta	2	6.45
5	Pyramidula pusilla, Cochlicella (Prietocella) barbara,	2	6.45
6	Truncatellina cylindrica	1	3.23
7	Xerotrichia conspurcata, Xerosecta (Xerosecta) reboudiana	2	
8	Oxychilus (Oxychilus) draparnaudi	1	3.23
9	Cernuella (Cernuella) virgata, Xerosecta (Xerosecta) promissa	2	6.45
10	Xerotrichia apicina, Theba pisana, Cochlicella (Cochlicella) acuta, Cochlicella (Cochlicella) conoidea	4	12.90
11	Rumina decollata, Microxeromagna armillata, Cantareus aspersus, Caracollina (Caracollina) lenticula, Ferussacia (Ferussacia) folliculus, Otala (Otala) lactea	6	19.35
12	Iberus gualtierianus alonensis, Sphnincterochila (Cariosula) baetica, Granopupa granum, Leonia mamillaris, Trochoidea (Xerocrassa) derogata	5	16.13
13	Hohenwartiana eucharista	1	3.23
14	Iberus gualtierianus globulosus, Otala (Otala) punctata	2	6.45
	Σ	31	100

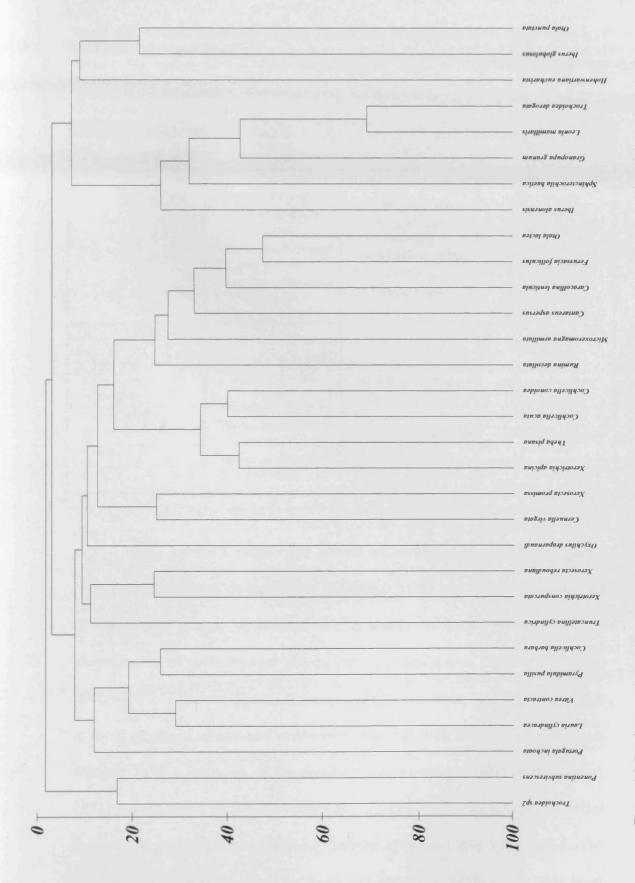


Figure 4.5. Dendogram of species from the sites (standardized species abundances). The species used are those remaining after the matrix has been reduced by removing species that constitute less than 25% of any sample. Species are on the x axis and Bray-Curtis similarities on the y axis.

Table 4.6. The three malacofaunal groups derived from interpretation of the cluster analyses of the species abundances matrix from the Biogeographical Sites with 3% and 25% reduction of species. The species for each malacofaunal group are shown for each reduction level. An asterisk indicates species that are present at both levels of reduction for each malacofaunal group (see text for details).

Malacofaunal group	Eastern/Xeric	Sand	Universal
	Species	Species	Species
Reduction level		200 - 200 ECM	
3%	*Granopupa granum *Sphincterochila baetica *Iberus gualtierianus marmoratus *Iberus gualtierianus alonensis	*Cochlicella acuta *Cochlicella conoidea Cochlicella barbara *Xerotrichia apicina *Theba pisana	Cecilioides jani *Ferussacia folliculus *Caracollina lenticula *Microxeromagna armillata *Otala lactea *Cantareus aspersus
n	4	5	6
25%	*Granopupa granum *Sphincterochila baetica Trochoidea derogata *Iberus gualtierianus marmoratus *Iberus gualtierianus alonensis	*Cochlicella acuta *Cochlicella conoidea *Xerotrichia apicina *Theba pisana	*Ferussacia folliculus Rumina decollata *Caracollina lenticula *Microxeromagna armillata *Otala lactea *Cantareus aspersu.
n	5	4	6

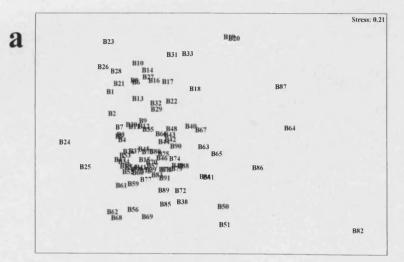
These analyses reduce the effects of rare species that make cluster interpretation difficult, or impossible (Section 4.2.2.2), and so the interpretations of the main groups described here probably provide the most robust identification of malacofaunal groups from the study area (Table 4.6). These groups are: (1) Eastern/Xeric, (2) Sand, and (3) Universal. Species membership in these groups is maintained at 3% and 25% reduction levels, with only three changes: (a) the inclusion of *Trochoidea (Xerocrassa) derogata* (Rossmässler, 1854) with Group 1 at the 3% level, (b) exclusion of *Cochlicella (Prietocella) barbara* (Linnaeus, 1758) with Group 2 at the 25% level, and (c) substitution of *Cecilioides (Cecilioides) jani* (De Betta and Martinati, 1855) at the 25% level with *Rumina decollata* (Linnaeus, 1758).

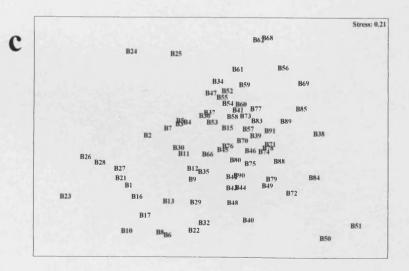
Further work is needed to establish if these malacofaunal groups constitute true species associations at short and long term temporal scales (Connell and Sousa, 1983; Townsend *et al.*, 1987; Luh and Pimm, 1993). This could be done by determining species interactions during dry and wet periods, over a number of years. At present the malacofaunal groups described here must be considered tentative and subject to revision as further data become available from this region (Section 8.5).

4.2.3. Ordination

The results of site ordination using Non-Metric Multidimensional Scaling (MDS) on the log_{x+1} species abundances from all sites support the findings using cluster analysis (Section 4.2.2). The 2-dimensional ordination diagram (Figure 4.6.a) shows some of the sites that are present in single-site cluster groups, such as Torre del Oro, Spain (Site B64) and Cabo Serdao Cavaleiro, Portugal (Site B87) as outliers. In general, the outliers are sites with low abundance and species richness. Most of the sites, however, are in one large group. Running the ordination with the outliers removed (Sites B19, 20, 64, 82 and 87; Figure 4.6.b), as well as running the ordination excluding the sites with total abundances of less than 200 (Sites B14, 18, 19, 20, 31, 33, 63, 64, 65, 67, 81, 82, 86 and 87, see Appendix 1; Figure 4.6.c) provides a wider spread of points in the MDS diagrams but does not provide alternative interpretations of the data. With such results for cluster and MDS, where low similarity levels resulted from cluster and a stress levels of 0.21 and 0.22 were produced by MDS (Figure 4.6.a, b, c), the two methods are best used together to complement each other (Section 3.7.2.2). The stress levels for the MDS are at the limit that still gives a potentially useful 2-dimensional picture (Clarke and Warwick,

1994), but it is clear that such a picture does not clearly express the factors involved in faunal differentiation.





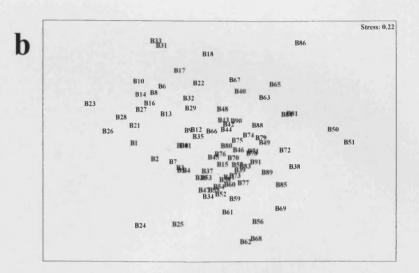


Figure 4.6. Multidimensional Scaling plots of \log_{x+1} species abundances. Data from all sites (a), Sites B19, 20, 64, 82 and 87 (outliers in plot a) excluded (b), and sites with abundances less than 200 excluded (B14, 18, 19, 20, 31, 33, 63, 64, 65, 67, 81, 82, 86 and 87) (c).

4.2.4. Linking environmental variables to species data (BIOENV)

The present study is the first that uses the BIOENV method with land molluscs; an overview of the method is given in Section 3.7.2.3. The best explanation of the species data using the environmental data of the present study is provided by climatic variables. These variables are the monthly mean of sunshine hours per day during the wet period months of December, January and February, and the annual mean absolute humidity (in g/m³) (Table 4.7).

Table 4.7. Combinations of variables that provided the largest harmonic rank correlations between the environmental and species similarity matrices using the BIOENV routine in PRIMER. The best combination is shaded. Abbreviations (in order of appearance): SJAN=Sunshine-January: Monthly mean (hours/day), SFEB=Sunshine-February: Monthly mean (hours/day), SDEC=Sunshine-December: Monthly mean (hours/day), ABHU=Absolute humidity: Annual mean (g/m³), SMAR=Sunshine-March: Monthly mean (hours/day), SSEP=Sunshine-September: Monthly mean (hours/day), SJUN=Sunshine-June: Monthly mean (hours/day), SOCT=Sunshine-October: Monthly mean (hours/day), TDJA=Temperature (diurnal variation)-January: Monthly mean (°C), SJUL=Sunshine-July: Monthly mean (hours/day). See Appendix 5 for details of all environmental variables used in the BIOENV analysis.

Number of variables	Variables in selection	Harmonic rank correlation		
4	SJAN, SFEB, SDEC, ABHU	0.336		
5	SJAN, SFEB, SMAR, SDEC, ABHU	0.336		
5	SJAN, SFEB, SSEP, SDEC, ABHU	0.333		
5	SJAN, SFEB, SJUN, SDEC, ABHU	0.328		
5	SJAN, SFEB, SOCT, SDEC, ABHU	0.325		
5	SJAN, SFEB, SDEC, TDJA, ABHU	0.324		
4	SJAN, SFEB, SMAR, ABHU	0.322		
5	SJAN, SFEB, SJUL, SDEC, ABHU	0.322		
4	SJAN, SFEB, SMAR, SDEC, ABHU	0.320		
5	SJAN, SFEB, SMAR, SSEP, ABHU	0.320		

The Harmonic rank correlation is low in comparison to studies that have used BIOENV in marine systems (Clarke and Warwick, 1994; Fa, 1998). The low correlation implies that some caution is required in assessing the possible importance that these variables may have in explaining patterns in the species abundances data. This highlights the caveat, when interpreting any multivariate analysis, that results need to be considered in the light of knowledge that exists

about the biology and ecology of the taxa under investigation (Eberhardt and Thomas, 1991; Whittaker *et al.*, 2001; Lepš and Šmilauer, 2003).

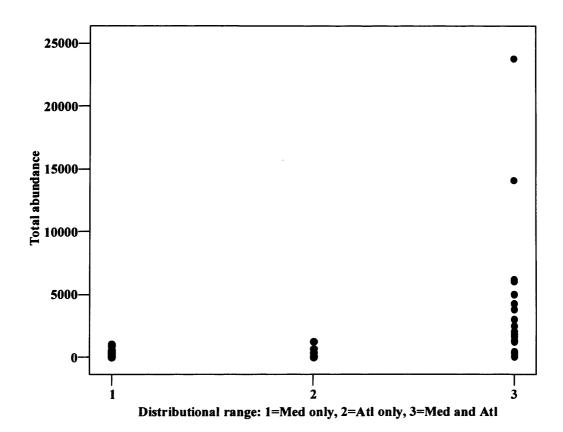
The majority of the variables used in BIOENV did not have much variation across the sites. Values for the coefficient of variation were quite low for most of the variables (Appendix 5) and this reduces the power of BIOENV to explain species abundances based on environmental variables clearly. Using BIOENV on small-scale variables from sites (such as amount of litter cover, soil components etc.) would probably provide more conclusive results than from the use of large-scale (or regional) variables as in this study. This becomes an issue of assessing the explanatory potential of environmental variables at differing scales and one that has many research possibilities. In addition, the use of large-scale variables (such as those from this study) would be more successful if a much larger biogeographical area were used (because of greater variance in the data) (Whittaker et al., 2001).

4.2.5. Distributions of the species, and number of sites at which they occur

Of the 94 species found at the sites, 27 were found only at Mediterranean sites, 30 only at Atlantic sites and 37 at both Mediterranean and Atlantic sites (Appendix 3). Cluster analysis carried out using species presence/absence, but excluding uniques (species that occur only at one site) resolves 7 groups (at 50% similarity level). Four are single-site membership groups; 3 of these are Atlantic sites, one a Mediterranean site. One group contains 7 sites, all are Mediterranean. The two largest groups both contain Atlantic and Mediterranean sites. A group with 29 sites has 4 Atlantic and 25 Mediterranean sites. The largest group (51 sites) has 35 Atlantic and 16 Mediterranean sites. These results (in particular groups 1 to 6) show limited

differentiation between the Mediterranean/Atlantic divide as used in this study (Section 3.7.2.5).

Figure 4.7. Total abundances of all species from the Biogeographical Sites with species categorized by distributional range. (Abbreviations: Med: Mediterranean, Atl: Atlantic). See text for details.

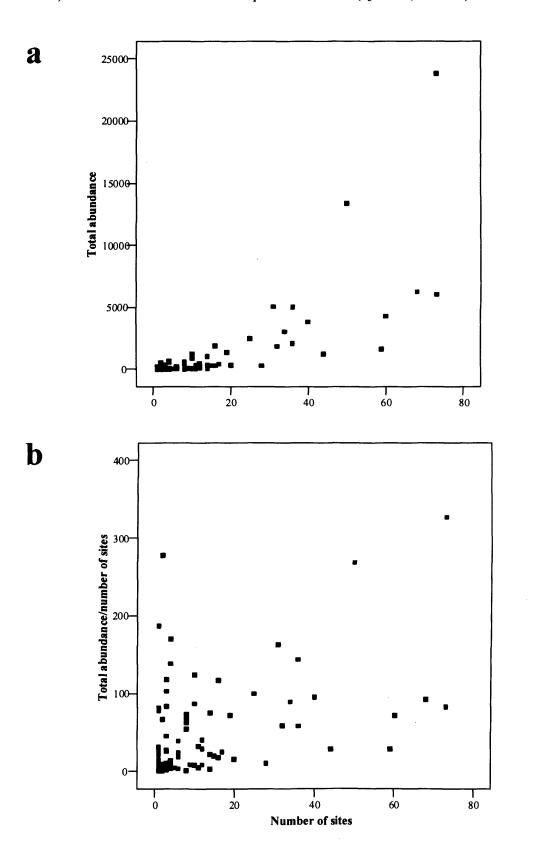


Species found only at Mediterranean, or only at Atlantic, sites had lower total abundances than species found at both (Figure 4.7.). To test the null hypothesis that there was no difference between the means of total abundances for each of the distributional range types (Section 3.7.2.5), the data were first tested for normality using the Kolmogorov-Smirnov test (Sokal and Rohlf, 1995). As this showed that the data were not normally distributed (Kolmogorov-Smirnov z=3.561, P<0.001, n=94), the Kruskal-Wallis test was used to test the hypothesis about difference of means (Sokal and Rohlf, 1995). The result of this test shows that there were highly significant differences in the means of the

abundances of species from these three types of species distribution ($\chi^2 = 28.7$; P < 0.001).

The number of sites at which each of the species was found is shown in Appendix 3. There was a significant positive correlation between the total abundances of the species and the number of sites at which species were found $(r_s=0.826, P<0.001, Figure 4.8.a.)$. This shows that the species with higher abundances were present at more sites than those with lower abundances. This positive correlation was diminished, but still significant, when total abundances were weighted by the number of sites at which each species was found. This allowed for the possibility that species that occur at more sites may have higher abundances because they have been sampled at more sites, rather than having higher total abundances $per\ se\ (r_s=0.482,\ P<0.001,\ Figure\ 4.8.b.)$. The results show that species with higher abundances occur at more sites even when their abundances are weighted in this way.

Figure 4.8. a. Correlation between species total abundance and the number of sites at which species were found (r_s =0.826, P<0.001). b. Correlation between total abundances (after weighting by dividing total abundance by the number of sites at which each species was found) and the number of sites at which species were found (r_s =0.482, P<0.001).



4.2.6. Species abundance models

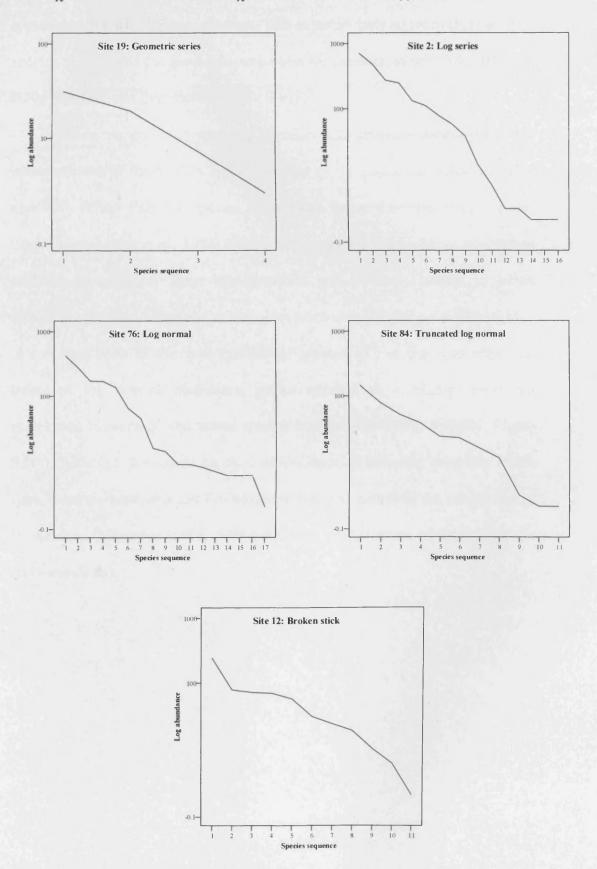
More than one model fitted the species abundance data from 55 of the 91 sites (60.4%, Table 4.8, Figure 4.9, Section 3.7.2.7). For two sites (B40 and B85) none of the models fitted the data.

Table 4.8. The best fitting species abundance models (based on *P* values of mathematical data fitting) for the sites. See Appendix 1 for site details. Abbreviations: GS=geometric series; LS=log series; LN=log normal; TLN=truncated log normal; BS=broken stick.

Site	Model(s)	Site	Model(s)	Site	Model(s)
B1	LR, TLN	B32	LN, TLN	B63	LS
B2	LS	B33	LN, TLN	B64	LS, LN, TLN
В3	LS, LN	B34	LS, TLN	B65	LN, TLN
B4	LS, LN, TLN	B35	TLN	B66	LN
B5	LN, TLN	B36	TLN	B67	LS, LN
В6	LN, TLN	B37	LS, TLN	B68	LN, TLN
B7	LS, LN, TLN	B38	TLN	B69	LN, TLN
B8	LN, TLN	B39	LN, TLN	B70	LS, LN, TLN
B9	LS, LN, TLN	B40	No model fit	B71	LS, LN
B10	LN	B41	LS	B72	LN, TLN
B11	LN, TLN, BS	B42	LN,TLN	B73	LS, LN
B12	BS	B43	LN	B74	GS, TLN
B13	LS, LN, TLN	B44	LS, LN, TLN	B75	BS
B14	LN, TLN	B45	LN, TLN	B76	LN
B15	LS, LN, TLN	B46	GS	B77	LS, LN
B16	LN	B47	LN, TLN	B78	LN, TLN
B17	LN, TLN	B48	LN, TLN	B79	LN, TLN
B18	LN, TLN	B49	LS	B80	LN, TLN
B19	GS	B50	TLN, BS	B81	BS
B20	GS	B51	TLN	B82	LS
B21	LN, TLN, BS	B52	LN	B83	LN
B22	LS, LN, TLN	B53	LS	B84	TLN
B23	LN, TLN	B54	TLN	B85	No model fit
B24	LN, TLN, BS	B55	LN, TLN	B86	LS
B25	LS, LN, TLN	B56	LN, TLN	B87	GS
B26	LN	B57	LS, LN, TLN	B88	LS, LN, TLN
B27	TLN	B58	LN	B89	LN, TLN
B28	LN, TLN	B59	LN, TLN	B90	LN, TLN
B29	LN	B60	LN	B91	LN, TLN
B30	LN, TLN	B61	LS, LN, TLN	100 0000	
B31	GS	B62	LN	11 11	

The sites may be divided into two groups: those fitting the geometric or log series, only, and all others (Sites B40 and B85 are not considered because they did not fit any of the models). Twelve sites (13.2% of total) are in the first group: Sites B2, B19, B20, B31, B41, B46, B49, B53, B63, B82, B86 and B87.

Figure 4.9. Species abundance models. Example plots of each of the models. Mathematical-fitting of the data: Site 19: χ^2 =3.9, df=3, P=0.30; Site 2: χ^2 =5.5, df=10, P=0.90; Site 76: χ^2 =16.4, df=10, P=0.10; Site 84: χ^2 =5.0, df=10, P=0.90; Site 12: χ^2 =3.2, df=9, P=0.95. See Appendix 1 for site details.



There are 77 sites (84.6% of total) in the second group. Analysis of the species abundance plots (Figure 4.9) indicates that the sites in the first group have several species with high abundances. This is particularly so when there are few species at a site and the geometric series best fits the data, as with Sites B19 and B20 (with four and five species, respectively).

Using standardized sampling (Section 3.5) provides robustness to the interpretations of the models. Sites described by the geometric series (e.g. B19 and B20) reflect that few species occur there, rather than that sampling was inadequate (Gaston *et al.*, 1997). Sites with high equitability indicate established mollusc assemblages. These interpretations are, however, subject to issues related to sampling, especially at low-abundance sites (Sections 4.4.2 and 8.1).

Prediction of the total number of species (S^*) at the sites using the truncated log normal abundance model resulted in a highly significant correlation between S^* and actual species numbers (r_s =0.923, P<0.001, Figure 4.10.). Although this could be used as evidence of adequate sampling at the sites, there are problems and limitations to using S^* including the calculation of its variance (Magurran, 1988, 2004 for review of discussion of these problems and limitations).

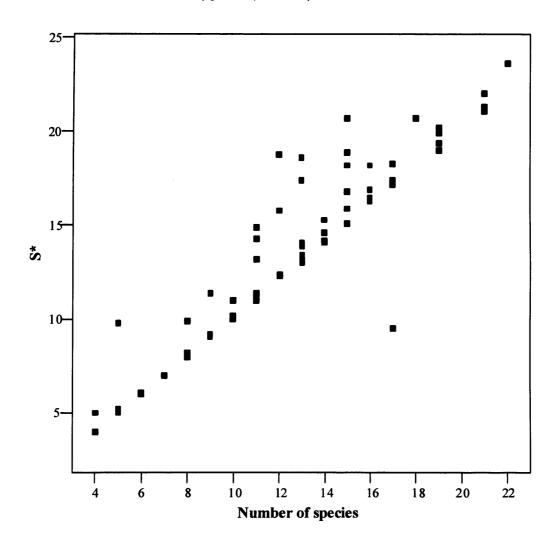


Figure 4.10. The number of species recorded, and species predicted (S*) from the truncated log normal abundance model for sites. (r_s =0.923, P<0.001).

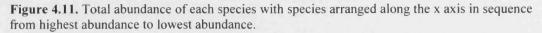
4.2.7. Commonness and rarity

The majority of species have low total abundances (Figure 4.11.). This is a well-documented finding in species abundance data, first reported by Fisher *et al.* (1943) and by many others since (Williams, 1964; Krebs, 1985; Hughes, 1986, McGill, 2003; Magurran, 2004). The species with highest total abundances are defined here as the commonest species, and those with lowest total abundances, as the rarest (Sections 3.7.2.4; 4.2.5 and Appendix 3). The data display a log normal pattern of species abundance (Section 3.7.2.7). Taken at smaller scales (rather than the regional context used here with data from all sites) this would indicate a mature and varied community (Sugihara (1980), Section 4.5.1.1). In

the present case, however, the pattern probably arises as a result of the statistical properties of large numbers (Magurran, 2004) and the Central Limit Theorem (Sokal and Rohlf, 1995). The commonest species from the study area are those with a Mediterranean-Atlantic distribution, and the rarest are those that have a Mediterranean only, or Atlantic only, distribution (Figure 4.12 and Table 4.9).

Table 4.9. The ten commonest (shaded), and ten rarest species from the Biogeographical Sites (using sampling methods from this study). Distributional range: M=present at Mediterranean sites only; A=present at Atlantic sites only; MA=present at both Mediterranean and Atlantic sites. (See Appendix 3 for species' authors).

Species	Total abundance (from all sites)	Rank	Distributional range	Number of sites at which present
Theba pisana	23810	1	MA	73
Cochlicella acuta	23383	2	MA	50
Ferussacia folliculus	6230	3	MA	68
Caracollina lenticula	6040	4	MA	73
Xerotrichia apicina	5056	5	MA	31
Truncatellina cylindrica	5020	6	MA	35
Otala lactea	4273	7	MA	60
Xerotrichia conspurcata	3813	8	MA	40
Microxeromagna armillata	3038	9	MA	34
Granopupa granum	2489	10	MA	25
Oxychilus sp2	2	74	A	1
Oxychilus sp3	2	74	M	2
Oestophora tarnieri	2	74	A	1
Candidula intersecta	2	74	A	1
Ganula gadirana	2	74	A	2
Acicula norrisi	1	75	M	1
Euconulus fulvus	1	75	A	1
Deroceras reticulatum	1	75	М	1
Trochoidea barceloi	1	75	М	1
Trochoidea sp3	1	75	A	1



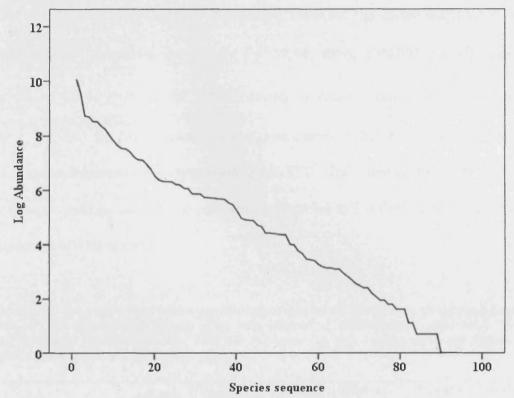
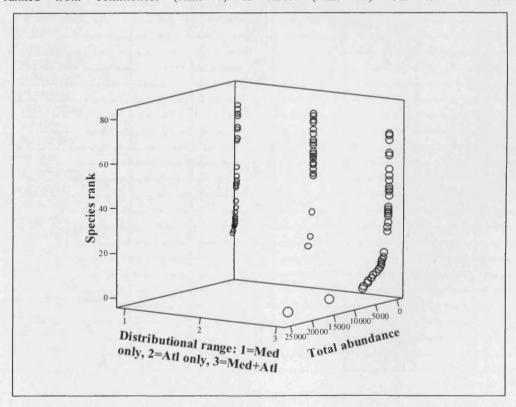


Figure 4.12. Three-dimensional plot showing the relationship between total abundance, species rank and distributional range (Med only=present at Mediterranean sites only; Atl=present at Atlantic sites only; Med+Atl=present at both Mediterranean and Atlantic sites). Species are ranked from commonest (rank 1) to rarest (rank 75). See text for details.



4.2.8. Numbers of species per family

The species were classified into 25 families. There are significant differences in the numbers of species per family (χ^2 37.44, df=6, P<0.001 for all sites. χ^2 21.20, df=6, P=0.002 for Mediterranean or Atlantic only sites. χ^2 17.60, df=4, P=0.001 for Mediterranean and Atlantic sites, Table 4.10). The majority of species belong to the Hygromiidae (46.8%). The interpretations of these analyses would be altered if membership of species to families as advocated by Anderson (2005) is used.

Table 4.10. The number (and percentage of total) of species per family from all sites and from each of the distributional ranges (Med only=present at Mediterranean sites only; Atl only=present at Atlantic sites only; Med and Atl=present at both Mediterranean and Atlantic sites). Systematics after Falkner et al. (2002).

	All sites	All sites	Med only or Atl only	Med only or Atl only	Med and Atl	Med and Atl
Family	Number	% of total	Number	% of total	Number	% of total
Aciculidae	1	1.06	1	1.75	0	0
Pomatiidae	1	1.06	1	1.75	0	0
Carychiidae	1	1.06	1	1.75	0	0_
Cochlicopidae	1	1.06	1	1.75	0	0
Pupillidae	1	1.06	1	1.75	0	0
Vallonidae	_ 3	3.19	2	3.51	1	2.70
Pyramidulidae	1	1.06	0	0	1	2.70
Chondrinidae	1	1.06	0	0	1	2.70
Vertiginidae	_ 3	3.19	2	3.51	1	2.70
Ferrussaciidae	4	4.26	1	1.75	3	8.11
Subulinidae	1	1.06	0	0	1	2.70
Testacellidae	1	1.06	0	0	1	2.70
Punctidae	2	2.13	2	3.51	0	0
Pristilomatidae	1	1.06	0	0	1	2.70
Euconulidae	1	1.06	1	1.75	0	0
Buliminidae	1	1.06	1	1.75	0	0
Oxychilidae	6	6.38	4	7.02	2	5.41
Parmacellidae	1	1.06	0	0	1	2.70
Milacidae	2	2.13	0	0	2	5.41
Limacidae	2	2.13	1	1.75	1	2.70
Agriolimacidae	4	4.26	3	5.26	1	2.70
Sphincterochilidae	2	2.13	2	3.51	0	0
Arionidae	1	1.06	0	0	1	2.70
Trissexodontidae	8	8.51	6	10.53	2	5.41
Hygromiidae	44	46.81	27	47.37	17	45.95
Totals	94	99.96	57	99.97	37	99.99

4.2.9. Beta diversity (β)

Over all sites β =7.77. Results for β are dependent on sampling effort, area and other factors (Harrison *et al.*, 1992; Heegaard, 2004; Magurran, 2004). The measure can be used to assess variation in species compositions in transects, gradients or entire sites (Section 3.7.2.8) and values may be lower for multiple samplings at single sites or locations than for inter-site comparisons. The high value for β from the 91 sites indicates a high degree of differentiation, or turnover (Section 3.7.2.8), in species composition at the sites (Magurran, 2004) and substantiates the results of cluster and MDS (Sections 4.2.2. and 4.2.3).

4.3. Summary of results

- 1. A total of 94 species were recorded from the 91 sites, with a mean number of 12.1 species (lower 95% CI: 11.2; upper 95% CI: 13.0), a mean total species abundance of 1068.8 (lower 95% CI: 843.8; upper 95% CI: 1293.7), a mean Shannon diversity of 2.380 (lower 95% CI: 2.253; upper 95% CI: 2.507), and a mean Simpson's diversity of 0.724 (lower 95% CI: 0.694; upper 95% CI: 0.754).
- 2. Clustering of the species abundances formed 34 groups. The largest group contained 16 sites. The remaining sites were in groups containing between one and seven sites; 16 of these groups contained only one site.
- 3. There are low levels of similarity between the land mollusc communities.
- 4. Three malacofaunal groups were identified: Eastern/Xeric, Sand and Universal.

- 5. The monthly mean of sunshine hours per day during the wet period of December, January and February, and the annual mean absolute humidity, provide the best explanation of the species data.
- 6. Of the 94 species, 27 were found only at Mediterranean sites, 30 only at Atlantic sites, and 37 at both.
- 7. Species with higher abundances were present at more sites than those with lower abundances.
- 8. Data from 12 sites fitted the geometric or log series species abundance models; 77 sites fitted the log normal, truncated log normal or broken stick models; two sites did not fit any of the models.
- 9. The majority of species have low total abundances.
- 10. The species were classified into 25 families. 46.8% of species belong to the Hygromiidae.
- 11. Beta diversity for data from all sites was 7.77.

4.4. Diversity analysis: discussion

4.4.1. Number of species, species abundances and species diversity

There was a total of 94 species from all the sites. This value is similar to the numbers from two other recent studies from the area (Table 4.11): Andalucia, Spain with 93 species (Arrébola, 1995) and La Comunidad Valenciana, Spain with 109 species (Martínez-Ortí, 1999). The high total abundances found at some of the sites are attributable to *Theba pisana* (Müller, 1774), *C. acuta* and *F. folliculus*. The first two of these are among the most abundant and wideranging of Mediterranean species (Pfleger and Chatfield, 1988; Giusti *et al.*, 1995) and occur in large numbers on vegetation during the Mediterranean dry period during which they aestivate. *Ferussacia folliculus* occurs in large

numbers under rocks and is generally active all year round but may become inactive during periods of particularly high temperatures and dryness when the interface between the soil surface and the underside of rocks, where it often occurs, dries (unpublished data).

In this study both the Simpson's and the Shannon indices were used and because there were some sites with high total abundances comprised of a few species (see above) it may be more appropriate to compare the sites with the Shannon index that is not as weighted as is Simpson's index towards the abundances of the commonest species (Magurran, 2004). The mean value of the Shannon index for the sites was 2.380, and the mean value for Simpson's index was 0.724, and although direct comparison to other studies is not possible because the same sampling methods have not been used, the value for the Shannon index is similar to those from many other land mollusc studies (Table 4.11; Section 8.2).

Table 4.11. Biotic data from selected sources. Abbreviations: H'=Shannon diversity index: (e)=log_e (2)=log₂; Ds=Simpson's diversity index; $\beta=$ Beta diversity. Data are not directly comparable because different sampling methods were used in these studies. See text for details.

Location	Nu	mber of s	pecies occ	urring sy	mpatrical	lly	Source
Factors North America		10-15					Solem (1984b)
Eastern North America Southeastern Australia			3-6				Solem (1984b)
Northwestern Australia			2-1				Solem (1984b)
South Africa			3-9				Solem (1984b)
Hawaii			5-8				Solem (1984b)
Polynesian and			J-0	<u> </u>			Soleiii (19840)
Micronesian Islands			5-1	2			Solem (1984b)
Taiwan			6-2	5			Solem (1984b)
East Africa			10-2				Solem (1984b)
West Europe			~20				Solem (1984b)
New Caledonia. New				i e e e e e e e e e e e e e e e e e e e	***		
Hebrides			15-2	21			Solem (1984b)
North-island (New Zealand)			58	}			Emberton et al. (1997)
Southeast-coastal							
Madagascar			52				Emberton et al. (1997)
	Total species	Mean sp/plot or site	unkn	(log lown)		β	
Kakamega (Kenya)	50	24.0		27		.08	Tattersfield (1998)
Cherangani (Kenya)	31	16.5		88		.88	Tattersfield (1998)
Mount Kenya (Kenya)	14	14.0		38		.00	Tattersfield (1998)
East Usambara (Tanzania)	64	21.8	2.9		2.94		Tattersfield (1998)
Ambioni (Tanzania)	29	14.3	2.0		2.04		Tattersfield (1998)
Miono (Tanzania)	6	6.0		70	1.00		Tattersfield (1998)
Pugu (Tanzania)	22	16.0	2.:		1.38		Tattersfield (1998)
Ngarama (Tanzania)	21	12.3	2.4		1.70		Tattersfield (1998)
Pindiro (Tanzania)	22	11.3		13	1.96		Tattersfield (1998)
Nanganga (Tanzania)	11	11.0		17		.00	Tattersfield (1998)
Masasi (Tanzania)	6	6.0	1.	18	ļ!	.00	Tattersfield (1998)
Sabah (Malaysian Borneo)	61	6.1			L	.58	Schilthuizen & Rutjes (2001)
Aegean Islands	90	12.7				.90	Cameron et al. (2000)
Crete	21	15.0			1	.40	Cameron et al. (2003)
Andalucia (Spain)	93	ļ			ļ		Arrébola (1995)
Comunidad Valenciana	109		ļ		i		Martínez-Ortí (1999)
(Spain)				r			
			H'(e)	H'(2)	Ds		
Southern Iberia (this study)	94	12.1	2.81	4.05	0.724	7.77	
	Mean species number from various habitat types		Mean β				
Sweden		24.5				Cameron (1995)	
England	38				36		Cameron (1995)
North Germany	31				77		Cameron (1995)
Central Germany		1.0 2.5			"	Cameron (1995)	
Poland			.60		Cameron (1995)		
North Italy	48				60		Cameron (1995)
Canada	17				<u>78</u>		Cameron (1995)
USA	51			3.	30		Cameron (1995)
Madeira	13.6					Cameron & Cook (2001)	

4.4.2. Sampling efficacy

The two main factors that determine the accuracy of species inventories are the scarcity of individuals (Gotelli and Colwell, 2001) and sampling efficacy

(Swan, 1970; Hortal *et al.*, 2006). Most species are scarce in any area that is sampled (McGill, 2003; Nijboer and Schmidt-Kloiber, 2004) resulting in strongly skewed patterns in species abundance distribution curves (Magurran, 2004, Sections 3.7.2.7 and 4.2.6). Sampling error can result in inaccurate species inventories and subsequent data analyses (Cameron and Pokryszko, 2004; 2005; Walther and Moore, 2005).

Efficacious sampling is especially important in structurally complex habitats, such as steppe and garigue, where species may be missed (Bishop, 1977). The sampling methods used in this study have been tested for efficacy in these habitats (Menez, 2001), improving the robustness of the results. Recent studies from other Mediterranean regions have used similar sampling methods; these include garigue and maquis sites on Aegean Islands (Cameron *et al.*, 2000), and maquis sites in Crete (Cameron *et al.*, 2003).

Other factors affect the accuracy of species inventories: (1) sampling of a site may be adequate, but the full inventory might still not be found because some species may be missed if sampling has only been undertaken once (Waldén, 1981; Pahl-Wostl, 1991), (2) some species are seasonal and abundances vary significantly over the year rendering them more difficult to find at some times of the year than at others (Kuźnik, 1997; Cameron and Pokryszko, 2005). The number of broods or generations per year affects the demographic compositions of species, and young individuals may be difficult or impossible to identify (especially slugs), and (3) some species, including slugs, are closely dependent on seasonal climatic effects and may be very difficult to find during some periods of the year (Quick, 1960; Newell, 1968; Runham and Hunter, 1970; Kerney and Cameron, 1979).

A limitation of many studies, including this one, is that they only provide a 'snapshot' of true diversity. Detailed studies that incorporate spatial and temporal replication at sites are labour-intensive and expensive, and there are no examples of this type of study from southern Iberia. Further fieldwork from this region may therefore alter the conclusions of the present study (Section 8.5).

4.5. Biogeographical analysis: discussion

4.5.1. Pattern and process at the local scale (site)

4.5.1.1. Species abundances

A few sites (13.2%) fitted the geometric or log series species abundance models, indicating the strong dominance of a few species (Section 3.7.2.7). The majority of sites (84.6%) fitted the log normal, truncated log normal or broken stick models, indicating diverse communities at these sites. These findings are similar to those of Barker (2005) from New Zealand where the data generally fitted the log normal model, and fitted the geometric series only in some less species-rich plots. Cameron and Pokryszko (2005) and Cameron *et al.* (2006) provide further examples of plots approaching the broken stick model from English woodland faunas.

4.5.1.2. Commonness and rarity

Seven of the ten commonest species from the present study belong to the Hygromiidae (Section 4.5.1.4), including *T. pisana* and *C. acuta* (Müller, 1774). The other three most common species belong to three distinct families. *Ferussacia folliculus* (Ferrussaciidae) is mostly found under rocks and logs, and *G. granum* (Chondrinidae) and *Truncatellina cylindrica* (Férussac, 1807) (Vertiginidae) on soil or among stones and rocks.

Some of the rarest species from the present study are endemics and include Acicula norrisi Gittenberger and Boeters, 1977, Ganula gadirana Muñoz, Almodovar and Arrébola, 1999 and Oestophora tarnieri (Morelet, 1854). Although some of these are rare per se (for example, A. norrisi, unpublished data), others have very patchy distributions (for example G. gadirana, unpublished data) and chance may be important in whether or not they are found. This has been reported by Cameron and Pokryszko (2004) for Vertigo alpestris Alder, 1838, and Cepaea hortensis (Müller, 1774) in Melitto-Carpinetum habitat in Białowieża Forest, Poland. An efficient and standardized collecting method, such as that used in the present study, is more likely to reduce sampling error (Section 4.4.2) than a less rigorous method, and so will increase the chance of finding these patchily-distributed species. Theba s. helicella is an example of a patchily-distributed species from southern Iberia. Based on material from El Alquián in Almeria, Spain, in the former Altimira collection, Gittenberger and Ripken (1987) concluded that the species may once have been introduced into southern Spain, but had since become extinct.

Sampling for the present study located the species at low abundance (13 individuals) at Retamar, Almeria, Spain (Site B21). During recent fieldwork by Menez (2006) the species was recorded from a single location in El Alquián, Spain (GPS: N36°50.992', W002°21.692'; date: 17-07-2002) (Figures 4.13, 4.14) where it attained densities of up to about 50/m². The re-discovery of this species at high density adds to the records of Puente *et al.* (1994), and Moreno and Ramos (2000; 2007) and highlights how commonness/rarity is dependent on factors such as permanence (Magurran and Henderson, 2003), dispersal

abilities (Kunin and Gaston, 1993; Maurer, 1999), range (Brown *et al.*, 1996), area searched and sampling methods used (Section 4.4.2).

Figure 4.13. Theba subdentata helicella (Wood, 1828) on ?Launaea sp. El Alquián, Spain.

Figure 4.14. Theba subdentata helicella (Wood, 1828) from El Alquián, Spain, in captivity.





4.5.1.3. Species distributions

The present study has shown that species with higher abundances were present at more sites than those with lower abundances, and that the commonest species found at the sites are those with wide distributions (Mediterranean-Atlantic species, Section 4.2.5). These results support the fundamental assumption of many metapopulation models that a relationship exists between the number of sites that a species occupies and its mean abundance in a region (Hanski and Gilpin, 1991; Hanksi and Gyllenberg, 1993).

The abundance-range relationship (He and Gaston, 1999) has been widely documented for many taxa (Hanski, 1982; Gaston and Lawton, 1990; Lawton, 1993; Gaston, 1996b). Gaston *et al.* (1997) identified eight hypotheses to explain this relationship: sampling artefact, phylogenetic non-independence, range position, resource breadth, resource availability, habitat selection, metapopulation dynamics and vital rates (but see Hartley (1998) who argues

that random species distributions alone may generate the relationship). Recent work has shown that insect data from *Acacia* tree canopies in Tanzania support the metapopulation dynamics and resource breadth hypotheses (Krüger and McGavin, 2000). Bock (1987) has shown that the relationship is not an artefact of species' conspicuousness, and that range size and local abundance are positively correlated, regardless of scale.

The results of the present study, obtained using robust sampling methods (Sections 3.5.1 and 3.5.2), support Bock's results for land birds, with possible criticisms that the relationship may have resulted solely from the ease of finding the commoner species over the rarer ones (Bock's species' conspicuousness) being largely refuted. This illustrates the importance of using adequate methods for sampling taxa such as land molluscs and other invertebrates that are difficult to find because of low numbers or cryptic behaviour, in order to demonstrate convincingly the abundance-distribution relationship (as well as other ecological relationships). Bock also suggests that the comparative study of the abundances of species instead of community structure might elucidate generalities in ecology and his results indicate that historical factors may play a major role in existing population dynamics.

Some of the species from the present study have limited distributions in Iberia (e.g. Sphincterochila spp. and Hypnophila malagana Gittenberger and Menkhorst, 1983). Others are restricted endemics (e.g. Gittenbergeria turriplana (Morelet, 1845) and G. gadirana), and at least one species, Leonia mamillaris (Lamarck, 1822), shows a possible relict distribution as a result of the previous continuity of the Betics-Rif mountain chain from southern Iberia and North Africa, and a subsequent vicariance event. Existing evidence for this

continuity has been recently substantiated by plate reconstructions that indicate late Cretaceous-Palaeogene congruence between African and European plates (Carbonell et al., 1998; Martínez-Martínez et al., 2006). During the Tertiary the western Mediterranean was involved in a series of events caused by the interactions of the African and European Plates (Giusti and Manganelli, 1984; Hrbek and Meyer, 2003). The eastern movement of the African Plate during the Oligocene or Lower Miocene caused detachment of the western portion of the Alpidic Chain (Rosenbaum et al., 2002; Rosenbaum and Lister, 2005) and its fragmentation into a series of micro-plates which subsequently moved in various directions in the Mediterranean, some towards North Africa, the Kabylias (Algeria), Italy (Calabro-Peloritan), Corisca and Sardinia (Alvarez, 1976; Giusti and Manganelli, 1984; Rosenbaum and Lister, 2004; Schettino and Turco, 2006).

Several disjunct land mollusc distributions have been reported from Mediterranean regions including *Pomatias, Tudorella, Hypnophila, Tacheocampylaea, Marmorana* and *Deroceras* (Giusti and Manganelli, 1984; Giusti *et al.*, 1995; Douris *et al.*, 1998; 2007) that have been attributed to microplate movement (as a result of faunas moving with these plates, Giusti and Manganelli, 1984), geographical isolation and habitat fluctuation, but further research is required to show whether there are disjunct species distributions in southern Iberia.

4.5.1.4. Familial composition

General trends in species compositions and diversity can be examined using taxon groups higher than species (Sale and Guy, 1992; Brown, 1995; Pik et al., 2002; Caruso and Migliorini, 2006; Moreno et al., 2008). Species may be

considered to be part of a hierarchically structured phylogeny (Felsenstein, 1985) and this has led to the development of methods for the measurement of diversity that take into account species' phylogenetic histories. These methods include Clarke and Warwick's taxonomic distinctness index (Warwick and Clarke, 1995, 1998).

Almost 50% of all species from the present study belong to the Hygromiidae (see Steinke *et al.*, 2004, Manganelli *et al.*, 2005 and Wade *et al.*, 2007 for phylogeny and discussion) and similar findings have been made for the British and northwest, mid-European and Aegean malacofaunas (Kerney and Cameron, 1979; Kerney *et al.* 1983; Mylonas, 1984). Seven of the commonest species from the present study belong to this family and if ecological and/or evolutionary success is measured by the number of extant representatives (Bradshaw, 1984; Futuyma, 1986; Gould, 2002), this is the most successful family.

Members of the Hygromiidae exploit a broad range of habitat resources, and although these resources may be considered as niches (Giller, 1984; Arthur, 1987) there are insufficient data to identify these niches or their breadths in southern Iberia accurately. These resources include the soil component and the underside of rocks and logs (*C. lenticula*), the soil surface and lower vegetation layers (*Xerotrichia conspurcata* (Draparnaud, 1801), *Xerotrichia apicina* (Lamarck, 1822) and *Otala* (*Otala*) *lactea* (Müller, 1774)), and the middle and higher vegetation layers (*T. pisana* and *C. acuta*) (unpublished data). There is evidence that the sizes of some of these species at different sites are related to the presence/absence of other land mollusc species as well as population

densities (unpublished data) supporting similar findings by Anderson *et al.* (2007) with the North American snail *Oreohelix cooperi* (Binney, 1838).

Evidence that land mollusc faunas are structured by competition is weak (Solem, 1984b; Cowie et al., 1995) and analysis of species data at family level provides a possible indication that competition may influence community structure (Cameron et al., 2003; Section 7.2.3.2). There are many examples in which very closely related and morphologically similar species co-exist. Cameron et al. (2003) suggested there may be interactive constraints on species richness in Cretan maquis based on the number of families and species (12 families and 27 species; ratio: 0.44). The species from maguis are more distantly related and morphologically distinct than in those in rainforest, and are present at higher densities and more continuous populations, which creates more opportunities for competition. Data for Cameroon (de Winter and Gittenberger, 1998) are 12 families and 97 species (ratio: 0.12), and for Sabah, Borneo (Schilthuizen and Rutjes, 2001) 14 families and 61 species (ratio: 0.23). In the present study, 25 families and 94 species were recorded (ratio: 0.26); a value midway between the Cretan and Cameroon estimates. These values are dependent on the methods used to collect the species data and are thus subject to the same caveats including area sampled and sampling efficacy (Section 4.4.2). Explanations other than competition for these ratios include adaptive and nonadaptive radiation (Cain, 1971; Mayo, 1983; Cameron et al., 2000; Bridle and Vines, 2006), dispersal ability (Jenkins and Buikema, 1998; Hubbell, 2001; Hardy and Sonké, 2004; Johansson and Ehrlén, 2003), as well as the time required for speciation to build up diversity in a region (the 'time-forspeciation-effect' of Stephens and Wiens, 2003; Section 4.5.2.4). Studies from

other regions including Turkey, where almost 80% of the fauna belongs to four families (Cook, 1997), Cameroon (de Winter and Gittenberger, 1998) and Madeira (Cameron, 1992; Cameron and Cook, 2001), have also demonstrated that the majority of species belong to a few families.

There is evidence that other ecological systems in southern Iberia show a similar pattern of family dominance. Menez *et al.* (2003) assessed the abundances and distributions of molluscs from 20 locations in southern Iberia. At each location land, intertidal and benthic ecological systems (Steele, 1985) were sampled for molluscs. In all systems families that were present at more sites, had higher abundances than those present at fewer sites, even when data were corrected for the number of sites at which families occurred. The number of families in the systems ranged from 13 (intertidal) to 46 (benthic –20m depth) but there was no significant difference in the proportion of families representing more than 1% of the total abundance in any of the systems (Table 4.12).

Table 4.12. Numbers of families representing >1% of total abundance in four systems from locations in southern Iberia. The differences in numbers of families representing >1% total abundance (as percentage) are not significant (Kolmogorov-Smirnov z=0.500; P=0.964). Source: Menez *et al.*, 2003.

	Number of families	Number of families representing >1% total abundance	Number of families representing >1% total abundance (as percentage)	
System				
Terrestrial	16	4	25	
Intertidal	13	3	23	
Benthic -10m	38	9	24	
Benthic -20m	46	12	26	

The proportions of species belonging to different families may be related to colonization, speciation and radiation (Russell-Hunter, 1983; Cook, 1997). These results, in conjunction with those of the present study (eight from 25

families: 32%), suggest that there may be an assembly rule for mollusc communities that applies in different ecological systems.

4.5.2. Pattern and process at the regional scale (study area)

4.5.2.1. Factors that influence distributions

The main factors that influenced the distributions of the land mollusc species were sunshine during part of the wet period (December, January and February) and annual humidity. In southern Iberia there is significant growth in vegetation, and significant mollusc activity (including egg laying) during these months. The results from the present study support those of many others that attempt to find determinant factors for land mollusc distributions (Section 1.2). Waldén (1981) reported that climatic variables (including rainfall) were among the factors explaining high diversity in wooded boulder slope habitats in southwest Sweden; Tattersfield et al. (2001) reported that malacofaunal variation in afromontane forests in Mount Kenya appeared to be more closely related to annual rainfall than to altitude per se or other environmental variables. Humidity was one of the best predictors of Carpathian Clausiliidae abundance (Sulikowska-Drozd, 2005) and of species composition in a Danubian floodplain (Čejka et al., 2008). Aubry et al. (2005) reported that mean annual temperature explained most of the relationships between number of species and altitude in southeast France, and Barker (2005) found that mean minimum temperature of the coldest month, annual mean temperature and annual solar radiation, were important determinants of community structure in New Zealand land snail faunas.

Climatic factors, including rainfall, also influence butterflies (Stefanescu et al., 2004) and vertebrates (Nogués-Bravo and Martínez-Rica, 2004) in the

Mediterranean, as well as other taxa in many other regions (Whittaker et al., 2001; Rodríguez et al., 2005: Langlands et al., 2006; Richardson et al., 2006). The results of the present study, however, are tentative and only provide an indication of what must be a much more complex picture. The reasons for this include: (1) there are probably many more variables that influence distributions, but that have not been measured, and (2) variables may have been collinear with unmeasured variables (Clarke, 1993; Clarke and Ainsworth, 1993), or may have been functions of other variables with unknown covariation (Sokal and Rohlf, 1995; Legendre and Legendre, 1998). An example is the effect of rainfall and temperature on soil properties (Benayas et al., 2004; Larchevêque et al., 2005). Extensive explorative data analysis using techniques such as Principal Components Analysis (ter Braak, 1995), multiple regression, or analysis of covariance (Sokal and Rohlf, 1995) may resolve variables that covary or that act as surrogates for a group of variables and this approach would be an improvement to a study such as the present study.

Humidity and the hours of sunshine during the months of the wet period are correlated to many biological processes and changes in the rates of these processes. It is possibly a subset of these processes, as well as humidity and hours of sunshine, that determine distributions. This means that the measured variables (humidity and hours of sunshine) also act as surrogate variables for those that are influencing distributions, and that remain unknown. The variables used in the present study probably act at the regional scale but also influence local-scale variables (Malanson *et al.*, 1992; Loehle, 1998; Johnson *et al.*, 2004). Measurement of local-scale variables would improve the accuracy of the findings of the present study.

4.5.2.2. The Mediterranean/Atlantic divide

The study area is in the Mediterranean Region (Section 2.2.1). The data from the present study show that there are some species that occur only in Atlantic coastal sites (30 species), or only in Mediterranean coastal sites (27 species) suggesting that the classic primary division of Iberia into Mediterranean and Atlantic regions (Section 2.2.1.) may not be adequate to differentiate between faunas from detailed biogeographical studies, such as this study. In these cases there may be a need to consider more defined, and restricted, biogeographical regions. Biogeographical analysis of the Helicoidea in Iberia (Puente *at al.*, 1998), for example, resulted in five major groupings. The sites from this study are located in three of these: the Mediterranean, the Extremadura-La Mancha-Andalusia, and the Lusitanian groups (Table 2.5). Using smaller biogeographical regions for assessment of faunal distributions is particularly relevant in marked heterogeneous regions such as southern Iberia.

4.5.2.3. Gamma diversity

Gamma diversity is a measure of regional diversity (Lincoln *et al.*, 1998; Rosenzweig, 1995) and this, calculated as the Shannon index for the entire species data set from the present study, is 4.05. This value approaches the value of 4.5 that Magurran (2004) states is rarely surpassed, and indicates that southern Iberia is a region of high diversity for land molluscs.

4.5.2.4. Species compositions

Species compositions, which may constitute communities or assemblages, can vary from location to location, and similarities (or dissimilarities) between them may be dependent on many factors including habitat heterogeneity, competition, climatic and historical factors (Diamond, 1975; May, 1984; Seifert, 1984;

Kikkawa, 1986). There were low levels of similarity in the land mollusc compositions from the sites in the present study. These results are similar to those of Cameron and Cook (2001) who reported that there were marked differences in the land mollusc faunas from coastal areas in southwest Madeira but much less differentiation from forested areas (Cameron and Cook, 1998).

There are no quantitative land mollusc data available for southern Iberia other than that from this study, so it is not possible to compare the data to other data from the region to assess levels of similarity from non-coastal sites. Dissimilarity at non-coastal sites, however, has been detected for other taxa in the region. Romero-Alcaraz and Ávila (2000), for example, found dissimilarity in beetle communities from the Sierra de Baza in southern Iberia that they attributed to habitat heterogeneity at the landscape level.

Cameron and Cook (2001) suggest that the differences at coastal localities in southwest Madeira may be as a result of climatic and sea-level changes in the Pleistocene/Holocene subjecting the areas to isolation and reconnection. The low levels of similarity in the land mollusc compositions from this study suggest that the heterogeneous habitats of southern Iberia may allow a large number of land mollusc species to co-exist in varied communities possibly controlled by historical and regional factors, including climate and geology (Blondel and Vigne, 1993; Cameron, 1995; Nekola and Smith, 1999).

Speciation is the process that ultimately generates species richness, but the time required for speciation to build up diversity in a region is rarely considered as an explanation for patterns of richness. This, the 'time-for-speciation-effect' of Stephens and Wiens (2003), may help account for high diversity in regions such as the Mediterranean.

There has been more time in southern Iberia, in relation to other regions such as mid- and northern Europe, for communities to develop, for the promotion of speciation and for species diversity to increase because the effects of glacial periods, that removed the faunas from large areas of Europe did not impact the area (Section 1.3). Taberlet et al. (1998) report small amounts of congruence in the distributions of ten taxa including mammals, amphibians and plants that they attributed to glacial periods. Species in southern Iberia, therefore, would not have been eliminated as a result of glacial events. Leading edge colonization during expansion after these events, however, may have led to homozygosity and spatial assortment of genomes in some species (Hewitt, 1996, 2004). There is, however, a long-standing debate over the effects that the Pleistocene glaciations may have had in promoting speciation in Europe and in other areas (Knowles, 2001; Ribera and Vogler, 2004). If there is a positive association as suggested by many workers, and taking into account that southern Iberia has been a glacial refugium on several occasions (Jaarola and Searle, 2004), these facts may partly explain the high endemism rates and high numbers of species of molluscs, and other taxa, in the region.

There is a highly significant decline in species similarities from Guardamar del Segura, Spain (Site B1) to Lagoa de Santo André Portugal (Site B91) (Figure 4.3) suggesting a climatic or environmental gradient acting across the region. This pattern is similar to that reported by Nekola and White (1999) for plants in North American forests. They developed the distance decay model, which describes how similarity in communities falls with decreasing environmental similarity with distance (topographic or climatic gradients), or by limits to dispersal and niche width differences among taxa (Oliva and González,

2005). Steinitz et al. (2006) showed that rainfall and geographical distance had negative effects on species similarity in land snails in Israel, and that large snails had a higher rate of decay in species similarity than small snails, which are better dispersers. Cameron and Pokryszko (2004) indicated that distance decay in similarity existed across faunas of northern, central and northwestern Europe, but that this decay is much less rapid than that in Mediterranean faunas.

Cameron and Pokryszko (2004) compared the faunas of Białowieża Forest in Poland with those of Kakamega Forest in Kenya (Tattersfield, 1996). Similar topography and major habitat types (riverine forests etc.) exist in both areas and sampling methods were very similar. Cameron and Pokryszko (2004) report that, although the faunas are very different taxonomically, results (number of species, rank abundance distributions etc.) are very similar. Beta diversity was also very similar (2.1 in Kakamega and 1.9 in Białowieża). Both of these areas have a Holocene origin and, as Cameron and Pokryszko (2004) identify, these faunas differ in diversity from older faunas, such as those from tropical forests that have more locally variable faunas.

4.5.2.5. Beta diversity

Among taxa, beta diversity is generally highest in those with the most restricted ranges and specialized habitats (Harrison *et al.*, 1992), and the low similarities of land molluscs in the region results in remarkably high beta diversity: 7.77. This confirms Cameron's (1995) prediction that beta diversity would be high in Mediterranean habitats where the fauna contains large or stenotypic species with poor powers of dispersal. (Cameron also highlighted the urgent need to collect diversity data from these areas, many of which are subject to long-standing degradation, and from which very little, or no data are available).

Beta diversity in the region is higher than, for example, that from a range of habitats (covering an area of about 98000 hectares) in Raukumara Peninsula in northeastern New Zealand (Barker and Mayhill, 1999). The result for the Raukumara Peninsula was 3.54 using sampling methods similar to those of this study. A value of 6.90 was reported by Cameron *et al.* (2000) for some Aegean Islands with similar habitat types to those from the present study, and Schilthuizen and Rutjes (2001) reported a value of 8.6 for a Sabah rainforest (Malaysian Borneo) although they state that this may be influenced by small sample sizes.

The results from this study substantiate the findings of Cameron *et al.* (2000) from some Aegean Islands who reported that the faunas from their study regions, which were about 250km apart, differed far more than faunas from north European forests that are spread over far greater distances. Northern faunas may be rich at the local level but are generally poor regionally as a result of the short time available for immigration since the post-Pleistocene (Cameron, 1995; Hausdorf, 2006).

Values for beta diversity are lower in northern temperate regions, and using data from Cameron (1995) a mean value of 2.3 (range 1.4-4.1) is derived from 34 surveys from seven countries (using between nine and 56 sites per survey). Although this value is only a guide, because of differences between surveys in habitat types, and distances between sites, it does illustrate the lower value from northern regions in comparison to those from southern Iberia.

4.5.2.6. The malacofaunal groups

The low levels of similarity in the land mollusc compositions from this study result in only a small number of groups of associated species, although there are as yet insufficient data to determine if these groups are true species associations (Section 4.2.2.2). Most of the species in these malacofaunal groups have Mediterranean-Atlantic distributions reflecting the presence of these species at numerous sites (Appendix 3). The Eastern/Xeric group is mostly composed of species that are found at sites in, and near, to Almeria, Spain, although a few species have Mediterranean-Atlantic distributions. This is the driest part of the study area (Font Tullot, 1984, 2000; Perry, 1997).

The Sand malacofaunal group is composed of high-abundance species and some of these (*Cochlicella* spp. and *T. pisana*) are commonly found together in very close proximity on vegetation. These species frequently aestivate together during the dry period on plant stems and leaves, forming dense concentrations (Section 7.2.2.1). In this condition *Cochlicella* spp. often occupies spaces between the shells of aestivating *T. pisana*. This malacofaunal group includes some the most abundant of all Mediterranean land molluscs (*T. pisana* and *Cochlicella* spp.). The Universal malacofaunal group includes common soil/under rock species, such as *F. folliculus* and *C. lenticula*, as well as the large helicids *O. lactea* and *C. aspersus*.

4.5.3. Comparisons with other regions

Land mollusc communities occur nearly worldwide with sympatric diversities ranging from single species (Subantarctic islands) to high diversity sites (Emberton, 1995b) such as Cameroon (97 species in 1km²: de Winter and Gittenberger, 1998), New Zealand (60 species in 4ha: Solem *et al.*, 1981) and Borneo (61 species in 1km²: Schilthuizen and Rutjes, 2001). The highest values for diversity of native land molluscs, in relation to total land area, are found on the islands of the tropical and subtropical Pacific (Cowie, 1996, 2001, 2004).

Mountainous regions and islands account for a significant portion of world land mollusc diversity (Solem, 1984b) and many large islands have diverse faunas including Japan, New Zealand, Cuba, Jamaica, New Guinea, and Madagascar (with endemism rates of over 90%, Solem, 1984b; Emberton, 1997).

Solem (1984b) stated that other than in New Zealand, sympatric diversity is usually only five to ten, and rarely exceeds 20 species. Solem and Climo (1985) suggested that land snail community richness rarely exceeds 12, although a number of studies have shown much higher values (Nekola, 1999 and Table 4.11). The mean number of species for the sites from this study was 12.1, a value in the mid-range by world standards (Cameron *et al.*, 2000) and similar to the values reported by Cameron and Cook (1998, 2001) for Madeira of 13.6 and 14.0, and 12.7 reported by Cameron *et al.* (2000) for the Aegean Islands using similar sampling strategies to this study.

Faunas of northern, central and northwestern Europe, and North America show little variation in species richness (Nekola, 1999) and although areas further south have much richer regional faunas, local communities are no richer than those of the north (Pokryszko and Cameron, 2005). The forest snail fauna of northern Europe is regionally poor (about 150 species, excluding slugs), but individual localities (clusters of sample sites within a few kilometres of each other) can be rich by global standards with up to 57 species (Pokryszko and Cameron, 2005).

Britain is a very uniform region for land molluscs (Cameron, 2002a) and individual, rich sites of less than 1km² may contain over 30% of the total national fauna (Cameron, 1998). Site by site comparisons of faunal similarity confirm the homogeneity of fauna in English calcareous woodlands (Cameron *et*

al., 2006), and Cameron and Pokryszko (2004) have shown that the faunas at sites in Białowieża forest (Poland) also show considerable uniformity.

Cameron (1992) reported that the native fauna of the Madeiran archipelago shows pronounced geographical differentiation. A result of the differentiation is that faunas of individual sites (even the best sites) are not rich, being on average poorer than those from equivalent sites in Europe and North America.

The malacofauna of southern Iberia shares characteristics with other Iberian faunas, with Mediterranean faunas in general, and with some eastern European faunas (Wells and Chatfield, 1992, 1995), in being diverse with many endemics (Section 1.3). Mediterranean faunas are more diverse, and include many more endemic species than those of central and northern Europe. This difference is largely attributable to glacial effects (Sections 1.3 and 4.5.2.4) with most northern temperate faunas having been significantly affected by Pleistocene climatic changes. Many areas were devoid of molluscs as recently as 14,000 years ago (Cameron, 1995) and most of the British fauna, for example, resulted from immigration from the continental mainland as deglaciation proceeded (Kerney, 1999), the southern faunas having formed the stock faunas for the northern regions (Cameron, 1995). The diversity and endemism levels in Iberia and the Mediterranean in general roughly fall between the low levels for some northern latitudes and the much higher levels that exist in some mountainous regions, islands and in the tropics.

Lange and Mwinzi (2003) reported high regional diversity in Arabuko Sokoke forest in East Africa, but the majority of species had low abundance. They ascribed this to a possible decline in abundance because of forest

disturbance. Emberton *et al.* (1997), however, reported that limited forest degradation showed no negative correlation with diversity in Tanzania, but was instead associated with greater diversity.

A notable feature of many of the high diversity forest studies, especially tropical rainforests, is the low abundances of many species. The data from Gabon (de Winter, 1995), Cameroon (de Winter and Gittenberger, 1998) and Sabah, Borneo (Schilthuizen and Rutjes, 2001) indicate high numbers of species with very low abundances. This contrasts with data from this study, as well as those from Crete (Cameron *et al.*, 2003) where species abundances were much higher. The faunas from plots from the Cretan study are very uniform in comparison to the rainforest faunas, with Sabah, Borneo having about three times as many species. The faunas of the Cretan plots are richer (Cameron *et al.*, 2003) (Table 4.13).

Table 4.13. The number of species in 400m² plots from Sabah, Borneo and Crete.

Number of species in 400m ² plots							
Location	Minimum	Maximum	Mean	Standard deviation	Source		
Sabah, Borneo	2	28	6.1	6.3	Schilthuizen and Rutjes, 2001		
Crete	9	20	15	3.2	Cameron et al., 2003		

There are several factors that must be considered in the validity of making comparisons between studies, and therefore between faunas. First, sampling methods are often very different between studies, and often there may not be any indication that sampling has been assessed for efficacy. Second, many studies include dead shells in their species matrices, in some cases they considerably out-number living animals. This may not qualitatively alter presence/absence at localities, but does so quantitatively. Cowie *et al.* (1995) reported that the majority of specimens collected in a survey from Hawaii were

dead, and only 10 of 16 taxa were collected live. An even higher proportion of dead shells was used in the analyses carried out by Schilthuizen *et al.* (2004) for limestone outcrops in Borneo; these were based on species data composed of greater than 99% dead shells. Very little is known about shell degradation rates and the factors that affect this (Cowie *et al.*, 1995) although some of the factors that contribute to degradation are known (e.g. pH and humidity) (Evans, 1972; Claassen, 1998; Reitz and Wing, 1999). Seddon *et al.* (2005) report that large numbers of specimens at some African forest sites reflect the high abundance of large dead shells that degrade less rapidly in base-rich soils. Nekola and Smith (1999) recognized that the number of species in samples from Wisconsin carbonate cliff communities may be exaggerated if shells persist in the soil for long periods. Cameron *et al.* (2003) have remarked how shell preservation in dry calcareous environments allow shells to persist for years, making it difficult to separate fresh from long dead shells, and Menez (2002b) showed that larger species degraded less rapidly than smaller ones in Mediterranean conditions.

Shells would be expected to degrade more rapidly in the acidic soil conditions typical of rainforests than in the basic soil conditions more prevalent in Mediterranean regions (Benayas *et al.*, 2004). Although abundances are low in many rainforest habitats, there is evidence that high abundances may be found where forest grows on limestone (Schilthuizen, 2004). These limestone habitat patches can support two to five times more species than non-limestone habitat ones with 100-1000 times as many shells. Although the increase in calcium carbonate *per se* may account for much of this increased abundance, decreased shell degradation may also be a factor. Third, comparisons are often made between studies that sample disparate habitat types, or between studies

that sample different numbers of habitat types. These comparisons rarely take into account habitat complexity as a determinant factor of diversity.

At present very few quantitative data exist that have been collected from comparably-sized areas. Table 4.14 lists the only studies from which data are available from areas of 1km², although these datasets are not entirely comparable because of different sampling methodologies. This type of data collection, extended to other regions, would, however, allow hypotheses about latitudinal and range effects to be constructed and tested.

Table 4.14. The number of species from studies conducted at sites of 1km².

Location	Number of species	Number of sites	Source
C	07	1	de Winter and
Cameroon	97	1	Gittenberger, 1998
Borneo	61	1	Schilthuizen and
		1	Rutjes, 2001
Crete	27	1	Cameron et al., 2003
French Guiana	34	1	Gargominy and
		1	Ripken, 1998*
Southern Iberia	12.1 (min:4; max:22)	91	This study

^{(*}This study was undertaken using soil samples only: 2x1m² quadrats at 20 locations for a total of 280 litres of soil).

4.6. Summary of Part One

91 sites, each 1km², were sampled from southern Iberia. A total of 94 species were recorded from the 91 sites. There was a mean number of 12.1 species (lower 95% CI: 11.2; upper 95% CI: 13.0) at the sites, a value in the mid-range by global standards and similar to values for Madeira and the Aegean Islands. There was a mean total species abundance of 1068.8 (lower 95% CI: 843.8; upper 95% CI: 1293.7), a mean Shannon diversity of 2.380 (lower 95% CI: 2.253; upper 95% CI: 2.507), and a mean Simpson's diversity of 0.724 (lower 95% CI: 0.694; upper 95% CI: 0.754). Of the 94 species, 27 were found only at Mediterranean sites, 30 only at Atlantic sites, and 37 at both. The majority of

species have low total abundances and species with higher abundances were present at more sites than those with lower abundances.

The species were classified into 25 families with 47% of species in the Hygromiidae. Species data from 12 sites fitted the geometric or log series species abundance models; 77 sites fitted the log normal, truncated log normal or broken stick models, but two sites did not fit any of the models. Clustering of the species abundances formed 34 groups. The largest of these contained 16 sites. The remaining sites were in groups containing between one and seven sites, and 16 of these groups contained only one site.

Low levels of similarity were found between the land mollusc communities, and beta diversity for data from all sites was 7.77. These results suggest that the heterogeneous habitats from the region allow a large number of mollusc species to co-exist in varied communities possibly controlled by historical and regional factors, including climate and geology. Faunas from this region differ far more than those from northern European faunas that are spread over greater distances. These northern faunas may be rich locally but are generally poor regionally reflecting the short time available for immigration since the post-Pleistocene.

Three main malacofaunal groups were identified: Eastern/Xeric, Sand and Universal groups. The monthly mean of sunshine hours per day during the wet period of December, January and February, and the annual mean absolute humidity, provided the best explanation of the species data.

Part Two: Habitat Structure

CHAPTER 5. INTRODUCTION

5.1. Scale

Over 70 years ago Boycott (1934) made the point (albeit indirectly) that considering scale was important in understanding land mollusc ecology. Since then, and particularly in the last two decades, the issue of scale, at both spatial and temporal levels, has become a central theme in ecology (Morris, 1987; Thorhallsdottir, 1990; Holling, 1992; Levin, 1992; Ray and Hastings, 1996; Blackburn and Gaston, 2002; Mayer and Cameron, 2003; Kneitel and Chase, 2004).

Problems related to scaling are central to ecological theory and the portrayal of an ecological system relies on the spatial, temporal, and organizational perspectives selected (Levin and Pacala, 1997; Bowyer and Kie, 2006), with different mechanisms controlling patterns of diversity at different scales (Scheiner et al., 2000; Mancera et al., 2005). In addition, species patterns and co-occurrences are scale-dependent (Finlayson, 1999; Petřík and Bruelheide, 2006), and species respond to habitat characteristics at different scales (Holland et al., 2004). In these issues land mollusc ecology has, until recently, lagged behind. The need for studies at a wide range of scales to allow global comparisons to be made, and for understanding patterns in diversity, was recognized by Cameron (2004). Nekola and Smith (1999) suggested that very little is known about small-scale diversity and community patterns in land molluscs. Although some studies have shown differences at small scales (Berry, 1973; Cameron, 1978; Nekola and Smith, 1999), the need for further research was highlighted by Cameron and Pokryszko (2005): 'One of the major challenges in the ecology and biogeography of terrestrial molluscs is to

determine the scales at which patterns of distribution occur, and the extent to which they correlate with environmental variation at small scales'.

5.2. Species-area effects

The number of species found at a location increases with search time and area, as described by the species-area model (Arrhenius, 1921; Hopkins, 1955; Kikkawa, 1986; Usher, 1991; Hart and Horwitz, 1991; Rosenzweig and Abramsky, 1993; Palmer and White, 1994; Brown, 1995; Rosenzweig, 1995; Magurran, 2004). This increase is apparent at scales ranging from 1m² to continental landmasses (Bell *et al.*, 1991; Watkins and Wilson, 1992; Ricklefs and Schluter, 1993) where the larger the area that is sampled the more species that are likely to be found (Schoener, 1974; Connor and McCoy, 1979; Hart and Horwitz, 1991; Brown, 1995; Rosenzweig, 1995; Lomolino, 2000).

Many hypotheses have been proposed to account for variations in the number of species collected from areas of differing size (Hart and Horwitz, 1991; Ulrich and Buszko, 2007) and these can be classified into three main groups: (1) Passive sampling models which assume that the number of individuals, normally correlated with area, is the causal factor, and that the species-area relationship results from increasing species richness in samples containing greater numbers of individuals (McGuinness, 1984; McGuinness and Underwood, 1986; Bolger et al., 1991), even in uniform environments (Connor and McCoy, 1979; Scheiner, 2004), (2) Fragmentation models which assume that area affects the temporal dynamics and relationships with other areas through effects on colonization, extinction, speciation and catastrophic disturbance (MacArthur and Wilson, 1967; Hart and Horwitz, 1991), and (3) Habitat diversity models which assume relationships between number of species

and heterogeneity, and between heterogeneity and area (Williams, 1964; Hart and Horwitz, 1991; Cramer and Willig, 2005).

Most explanations for the species-area relationship are based on the area per se hypothesis and the habitat diversity hypothesis (Ricklefs and Lovette, 1999; Scheiner, 2003, 2004; Triantis et al., 2005a, b). The area per se hypothesis assumes that the number of species found at a locality increases with increasing area sampled because the majority of species are rare and will not occur in all sampled areas (Nilsson et al., 1988; Hart and Horwitz, 1991; Storch et al., 2003). These species will be sampled only in larger areas (even if their spatial distributions are random). The habitat diversity hypothesis (Williams, 1964; MacArthur and Wilson, 1967; Hart and Horwitz, 1991) assumes that larger areas have more habitat diversity, and therefore more species, than smaller areas.

Extinction-colonization dynamics (Rosenzweig, 1995; Hanski, 1999), high rates of dispersal among less isolated habitats decreasing the probability of extinction, or the rapid recolonization of species following any local extinctions that occur (Brown, 1995; Gilpin and Hanski, 1991), impact metapopulation structure and may affect species-area relationships (Storch *et al.*, 2003). Other factors include evolutionary history, extinction and migration (Coleman *et al.*, 1982; Wissel and Maier, 1992; Adler and Lauenroth, 2003; Heegaard, 2004; Roy *et al.*, 2004; Lawson and Jensen, 2006). An extension of the species-area theory is the species-energy theory that is obtained by replacing 'area' with 'available energy' in the model (Wright, 1983).

Triantis et al. (2003) have pointed out that many authors have implied that the area per se and the habitat diversity hypotheses may not be mutually

exclusive, and that area and habitat diversity are strongly interconnected. Triantis *et al.* (2003, 2005a, b) proposed the Choros model that joins area and habitat diversity, expressing their combined effects, by multiplication of a region's area with the number of different habitat types in the region. The authors assessed the model using 22 published datasets for different faunistic groups and found that it fitted the data better than the species-area model in 20 cases. Those where the datasets did not fit were snails and beetles which the authors ascribed to the way the habitat was defined using vegetation sampling. Other datasets for snails and beetles, however, fitted the Choros model better than the species-area model. The Choros model, used by Panista *et al.* (2006), better explained species richness patterns than area alone for plants in the Aegean archipelago.

Although there are recently published studies on land mollusc diversity from delimited sampling areas (e.g. Waldén, 1981; Emberton, 1995a, 1997; Tattersfield, 1996; de Winter and Gittenberger, 1998; Cameron, 1973, 2002b, Cameron and Cook, 2001; Cameron *et al.*, 2000) these have not specifically considered the data from the same locations at multiple scales. This study is the first attempt to assess these relationships using a hierarchical nested sampling design.

5.3. Habitat structure and the habitat structure model

In both natural and disturbed environments there is substantial variance in habitat structure at spatial scales of 1m² to 10,000m² (Stowe and Wade, 1979; Bell *et al.*, 1993). This includes vegetation architecture and quantities, and types, of rocks and logs (Grime and Blythe, 1969; Price *et al.*, 1995; Heller, 2001; Luchtel and Deyrup-Olsen, 2001; Olabarria and Chapman, 2001; Ondina

and Mato, 2001). Waldén (1981) showed that microhabitat differentiation (which he defined as variation in litter depth, moisture and shelter availability for molluscs) of woods and boulder slope habitats in southwestern Sweden affected diversity, and Cowie *et al.* (1995) showed that environmental variability at a scale of 0.09m² significantly influenced distributions of land snails in a montane habitat in Hawaii.

The variability of type and quantity of habitat structure has been associated with increased number of species of other invertebrates; Benton *et al.* (2003) reported increased diversity among farmland invertebrates at both 1km² and 25km² scales, than at smaller scales. Heterogeneous and complex habitats provide refuges from predation and competition effects for many taxa including frogs (Gunzburger and Travis, 2004), lizards (Petren and Case, 1998), subtidal limpets (Fletcher and Underwood, 1987), shrimps (Macia *et al.*, 2003; Meager *et al.*, 2005), crabs (Buck *et al.*, 2003), copepods (Hicks, 1980), intertidal macroinvertebrates (Edgara *et al.*, 1994) and damselflies (Elkin and Baker, 2000). Many species exhibit positive selection for highly heterogeneous habitats (Hicks, 1985; Gee and Warwick, 1994; Jensen *et al.*, 2003; Stoner and Titgen, 2003; Almany, 2004; Hernández *et al.*, 2005; Sass *et al.*, 2006).

The association of vegetation with some invertebrate taxa has been demonstrated (Dennis, 2004; Brose, 2003; Fleishman *et al.*, 2005) but associations are not fully elucidated for land molluscs. Most land molluscs feed on a wide range of live and dead plants (Rollo, 1988; Sternberg, 2000; Ondina and Mato, 2001; Speiser, 2001; Horsák and Hájek, 2003). This suggests that vegetation may be a determinant factor of diversity and abundance, not only as a food resource but also by providing shelter and micro-habitats (Russell-Hunter,

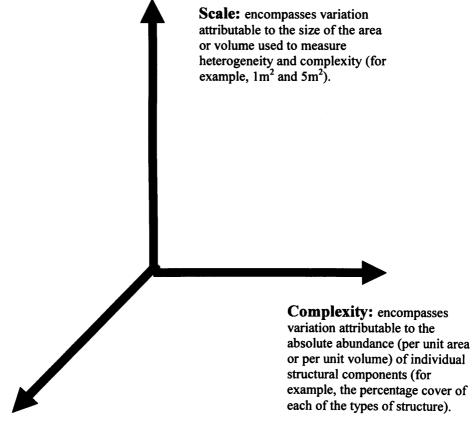
1964; Waldén, 1981; Alpert, 1991; Price et al., 1995; Cook, 2001; Speiser, 2001; Peeters, 2002). The spatial structure of vegetation influences the behaviour of individual organisms as well as the population dynamics of resident populations (Haysom and Coulson, 1998; Frietas et al., 2002; Despland, 2003; Watson et al., 2004). Some land mollusc studies have demonstrated minimal influence of vegetation on diversity and distribution (Cowie et al., 1995) whilst others have shown that vegetation is highly significant in influencing diversity and distribution (Proschwitz, 1993). Barker and Mayhill (1999) showed that land mollusc abundance and diversity in northeastern New Zealand increased with vegetation diversity. They proposed that localities with higher vegetation diversity have higher complexity and more varied substrate than localities with lower vegetation diversity.

Labaune and Magnin (2002) reported that land snails did not appear to be dependent on plant species. Relationships between plants and land molluscs may be more as a result of the micro-habitats provided by vegetation structure rather than the plants themselves (Kiss and Magnin, 2003). In addition, Horsák et al. (2007) have suggested that the associations they reported from western Carpathian Spring Fens may have been governed more by historical development than ecological gradients. Beyer and Saari (1978) showed that the strong association between slugs and grass in wooded areas of New York was related to the shelter provided by the grass. These studies confirm earlier reports of associations between plant taxa and land molluscs (Shimek, 1930; Boycott, 1934; South, 1965; Beyer and Saari, 1977) and that in some cases these associations are important in structuring assemblages (Grime and Blythe, 1969; Peters et al., 2007). Dillon (1980) predicted snail presence with 78% accuracy

in an Arizona canyon using vegetational cover alone. Associations between plant taxa and mollusc species, in conjunction with high sensitivity to environmental variation, have enabled land molluscs to be used as indices of both vegetation types and climate in the reconstruction of Quaternary assemblages (Davies and Grimes, 1999; Moine *et al.*, 2002). Similar levels of prediction have been made for other taxa that have low dispersal abilities, including spiders and small insects (Greenstone, 1984; Ward and Lubin, 1993; Dennis *et al.*, 1998; Rypstra *et al.*, 1999; McNett and Rypstra, 2000; Romero and Vasconcellos-Neto, 2005), and millipedes and woodlice (David *et al.*, 1999).

Habitat structure affects the abundance and the diversity of species of many taxa in many different systems (MacArthur and MacArthur, 1961; MacArthur et al., 1966; Abele, 1974; Menge and Lubchenco, 1981; Coul and Wells, 1983; Abramsky et al., 1990; Werner et al., 1983; Ward and Lubin, 1993; Halaj et al., 1998; Lohrer et al., 2000; Taniguchi and Tokeshi, 2004) but as McCoy and Bell (1991), and more recently Beck (2000) and Kostylev et al. (2005), have indicated, different elements of habitat structure, such as the types (e.g. vegetation, soil and rocks) and quantities of these types, are often confounded making it difficult to compare results between studies. To solve this problem, McCoy and Bell (1991) developed a model of habitat structure that has three axes and that they considered to 'encompass the breadth of ecological relationships implied by 'habitat structure' and related terms' (Figure 5.1). The axes are defined as: (1) the heterogeneity axis that encompasses variation attributable to the relative abundance (per unit area or per unit volume) of different structural components (i.e. types of structure such as rocks, logs and

vegetation); (2) the *complexity* axis that encompasses variation attributable to the absolute abundance (per unit area or per unit volume) of individual structural components (for example, the percentage cover of each of the types of structure); and (3) the *scale* axis that encompasses variation attributable to the size of the area or volume used to measure heterogeneity and complexity (for example, $1m^2$ and $5m^2$).



Heterogeneity: encompasses variation attributable to the relative abundance (per unit area or per unit volume) of different structural components (i.e. types of structure such as rocks, logs and vegetation).

Figure 5.1. A graphical model of the components of habitat structure adapted from McCoy and Bell (1991).

This model of McCoy and Bell (1991) has been used by Downes *et al.* (1998) to study the effects of habitat structure and local species diversity in an upland stream in southeastern Australia, by distinguishing between the effects of increasing habitat structure by the addition of physical elements (to increase complexity) from those of adding different types of habitat structure (to increase heterogeneity), at scales 'relevant to the biota' (using combinations of blocks with surface areas of 1,012cm²). Downes *et al.* (1998) reported that: '.. our study strongly suggests that resources related to habitat structure have a regulatory influence on species richness, and that this regulation is both strong and precise'. They showed that using the model allowed the importance of different elements of habitat structure to number of species, such as gaps in the substrate of <1mm and the densities of algal fronds, to be identified.

Beck (2000) used the model to study the independent effects of habitat complexity and heterogeneity on rocky intertidal gastropods in Botany Bay, Australia and showed that the complexity of habitats positively affected the number of species and their abundances. The study also showed that the effects of heterogeneity on the number of species and their abundances were independent of their complexity. Kelaher (2003a) studied the effects of habitat structure on gastropod assemblages on a rocky shore in Sydney, Australia using the model and showed that the vertical scale component of structure had significant effects on the associated assemblages. In a similar study, also in Sydney, Kelaher (2003b) showed that there were significant negative correlations between the density of algal fronds (complexity) and the number of species and species abundances of gastropods. Kelaher interpreted this as indicating the existence of distinct upper thresholds in the relationship between

complexity and the number of species. Schreider *et al.* (2003) used the model to study the effects of height on the shore and habitat complexity on amphipod abundance in rock pools in New South Wales, Australia, and determined that complexity did not influence abundance.

The main aim in Part Two is to assess the effects of habitat heterogeneity and complexity on the number of species and species abundances at three different scales (1m², 5m² and 20m²) in three habitat types, to determine if these effects are scale-dependent and habitat-specific, and to determine if there are variations in these in relation to the wet and dry periods of the year (Section 1.5). Hypotheses were constructed and tested using correlation and ANOVA analyses. These hypotheses and methods are detailed in the following chapter.

CHAPTER 6. METHODS

6.1. The study area

The study area is southern Iberia; defined in this study as that part of the Iberian Peninsula below the 38° line of latitude, and which includes Gibraltar, southeast Spain and southern Portugal (Section 3.1).

6.2. Selection of sites

Most of the sampling sites were within 100km from Gibraltar; this allowed a site to be reached and sampled on the same day (Figure 6.1 and Table 6.1). Part Two investigations aim to study the effects of habitat structure on the number and abundances of species; it was therefore not necessary to use a site-selection system that systematically included as much area as possible in southern Iberia, as was the case for the previous biogeographical work (Section 3.2). As with the Biogeographical Sites, a distance of not more than 5km from the coast was used as the cut-off. This was to standardize, as far as possible, any effects of proximity to the coast on the data. Sites were selected by driving along the coast and stopping where the following criteria were met:

- (1) an area of approximately 1km² with no man-made structures, or only a minimal number of these,
- (2) as little anthropogenic disturbance as possible (visual assessment of buildings, roads, other construction etc.), and
- (3) as much as possible of one of the habitat types under study: sand, steppe and garigue (visual assessment).

Figure 6.1. Iberia, showing extent of the 38° line of latitude (box) and detail of boxed area showing the positions of the sites (see Table 6.1 for details of sites, and Appendix 6 for photographs of sites).

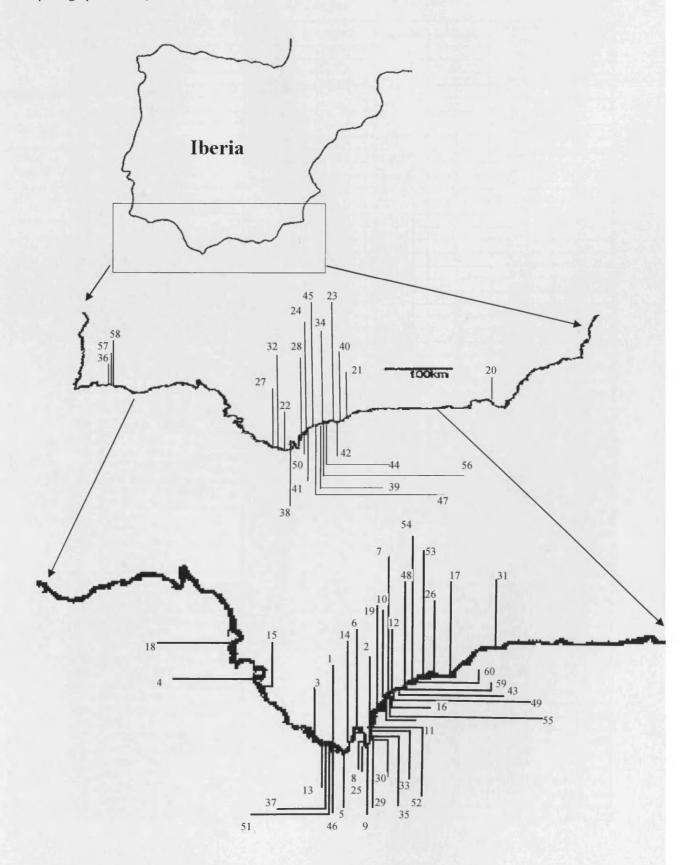


Table 6.1. The sites used in Part Two of the study, showing sampling date, latitude and longitude of each site (measured in minutes and degrees), altitude (metres above sea level), habitat type and sampling period (wet or dry).

Site	Site Name	Date	Latitude	Longitude	Altitude	Habitat	Period
No.	Diava da las Langas Casia	Sampled	2602607	00539317	3	Type	Wet
S1	Playa de los Lances, Spain	20/10/2003	3602687	00538217	2 25	Sand	Wet
S2	Pinar del Rey, Spain	25/10/2003	3614693	00323998	23	Sand	Wet
S3	Sancti Petri, Spain	31/10/2003 01/02/2004	3623133 3629174	00612393		Sand	
S4	Cadiz, Spain			00613941	5	Sand	Wet Wet
S5	Punta Paloma, Spain	08/03/2004	3604643			Sand	
S6	La Linea, Spain	20/03/2004	3609308	00520349	3	Sand	Wet
S7	Costalita, Spain	20/11/2004	3627471	00502594	2	Sand	Wet
S8	Western Beach, Gibraltar	27/12/2004	3609164	00521073	2	Sand	Wet
S9	Talus Slopes, Gibraltar	01/01/2005	3608202	00520469	40	Sand	Wet
S10	Playa del Negro, Spain	15/01/2005	3619853	00514423	2	Sand	Wet
	Sotogrande, Spain	29/05/2004	3616348	00517097	1	Sand	Dry
S12	Bahia Dorada, Spain	14/08/2004	3624215	00511397	2	Sand	Dry
S13	Zahara de los Atunes, Spain	21/08/2004	3609005	00551851	3	Sand	Dry
S14	Carteia, Spain	04/09/2004	3611085	00524779	5	Sand	Dry
	Conil de La Frontera, Spain	04/02/2005	3617909	00608079	15	Sand	Dry
	Torre Real, Spain	12/06/2005	3620215	00450611	2	Sand	Dry
	Malaga, Spain	19/06/2005	3638767	00430512	30	Sand	Dry
	Sanlúcar de Barrameda, Spain	25/06/2005	3646682	00622248	2	Sand	Dry
	Alcaidesa, Spain	18/07/2005	3614387	00518553	2	Sand	Dry
	El Ejido, Spain	29/07/2005	3642246	00249951	2	Sand	Dry
	La Zagaleta, Spain	06/10/2003	3633168	00501748	85	Steppe	Wet
	Algeciras, Spain	15/11/2003	3606158	00527691	40	Steppe	Wet
	Benahavis, Spain	22/11/2003	3629942	00501090	200	Steppe	Wet
	La Cañada, Spain	20/12/2003	3632196	00452184	50	Steppe	Wet
	Little Bay Slopes, Gibraltar	11/01/2004	3606905	00520983	15	Steppe	Wet
S26	Mijas, Spain	12/04/2004	3634895	00436850	100	Steppe	Wet
S27	Facinas, Spain	22/04/2004	3609062	00541787	30	Steppe	Wet
S28	Campamento, Spain	27/11/2004	3611461	00521100	5	Steppe	Wet
S29	Windmill Hill Flats, Gibraltar	18/12/2004	3607471	00520623	50	Steppe	Wet
	Half Moon, Gibraltar	03/01/2005	3608566	00520419	5	Steppe	Wet
S31	Torrox, Spain	09/07/2003	3646356	00356863	75	Steppe	Dry
	La Janda, Spain	02/08/2003	3604927	00537339	3	Steppe	Dry
S33	Upper Rock, Gibraltar	16/08/2003	3607329	00520561	325	Steppe	Dry
S34	Cove Beach, Spain	05/06/2004	3624867	00509783	2	Steppe	Dry
S35	Western Slopes, Gibraltar	03/07/2004	3608265	00520986	200	Steppe	Dry
	São Bras, Portugal	19/07/2004	3707837	00753755	70	Steppe	Dry
	Betis, Spain	30/08/2004	3605096	00541632	120	Steppe	Dry
	Miraflores, Spain	05/09/2004	3612664	00524677	10	Steppe	Dry
	Sabinillas, Spain	11/09/2004	3625593	00510951	70	Steppe	Dry
	Delfimar, Spain	12/09/2004	3625926	00506812	2	Steppe	Dry
	El Higueron, Spain	19/10/2004	3611799	00520804	4	Garigue	Wet
	Casares, Spain	11/10/2003	3624085	00514134	75	Garigue	Wet
	Castellar de la Frontera, Spain	29/11/2003	3618872	00527415	175	Garigue	Wet
	Playa del Seghers, Spain	07/12/2003	3624984	00510210	15	Garigue	Wet
	San Roque, Spain	03/01/2004	3614852	00520614	20	Garigue	Wet
	El Bujeo, Spain	10/01/2004	3605585	00530824	320	Garigue	Wet
	Serrania Bermeja, Spain	28/02/2004	3630991	00444857	210	Garigue	Wet
S48	Torreguadiaro, Spain	11/12/2004	3618367	00515738	2	Garigue	Wet
	Martagina, Spain	22/01/2005	3620598	00515430	50	Garigue	Wet
S50	Santa Margarita, Spain	30/01/2005	3612819	00520609	25	Garigue	Wet
	Bolonia, Spain	24/05/2003	3605969	00543935	4	Garigue	Dry
S52	Mediterranean Steps, Gibraltar	29/05/2003	3607046	00520426	300	Garigue	Dry
S53	Muela, Spain	28/06/2003	3615833	00600048	150	Garigue	Dry
	Cala Sardina, Spain	15/07/2003	3618522	00515589	15	Garigue	Dry
	Aldea Beach, Spain	24/08/2003	3020146	00514301	2	Garigue	Dry
	Manilva, Spain	30/08/2003	3623543	00515634	40	Garigue	Dry
	Monte, Portugal	21/07/2004	3707748	00753872	65	Garigue	Dry
	Alfaroba, Portugal	28/07/2004	3707657	00753768	60	Garigue	Dry
	Guadalmansa, Spain	25/09/2004	3627228	00503466	2	Garigue	Dry
S59							

The habitats were classified based on Rivas Goday (1968), Rivas-Martinez (1973, 1981, 1987), Polunin and Walters (1985), Polunin and Smythies (1988), Arroyo and Marañón (1990) and the Interpretation Manual of European Union Habitats (Anon., 1995). The difficulty of clearly differentiating these habitat types is apparent in this literature and often there may be a gradation of one habitat type into another. Additionally, there is some discrepancy in the literature as to definitions of the habitat types.

There are extensive areas of sand habitat in southern Iberia, including dunes, that form parts of coastal areas (Serra and Ros; 1989; Pascual, 1991). Steppe and garigue are typical coastal habitats in southern Iberia and are generally considered to be part of a continuum of Mediterranean habitat types that grade through steppe, garigue and maquis to forest. Many of the factors required to effect changes in this continuum are closely associated with humans and their animals (Serra *et al.*, in press). Maintenance of particular habitats (i.e. stopping progression in the continuum) is also largely dependent on human activity, including fire, (Faulkner and Hill, 1997; Blondel and Aronson, 1999; Grove and Rackham, 2001), although no evidence of the use of fire was detected at any of the sites used in the present study.

The three habitat types were chosen to represent commonly occurring and typical habitat types in southern Iberia. They are also ones with which the author is familiar. The following characterizing points were used to identify the habitats:

Sand: Areas with annuals, grasses and some bulbous species, and with a substratum of sand. These may be sand dunes but also expanses of coastal areas

with no dunes. Plants include: squill (Scilla), sea holly (Eryngium), plantain (Plantago), sedge (Cyperus) and vetch (Hedysarum).

Steppe: Areas with mostly annuals and perennials with deep root systems, some areas are predominantly grassy with many species of annual grasses. Plants include: asphodels (*Asphodelus*), clovers (*Trifolium*), anemonies (*Anemone*), daisies (*Bellis*) and bulbous plants (*Iris*, *Allium*, *Narcissus*).

Garigue: A widespread Mediterranean habitat type also known as *tomillares* (Spain), *phrygana* (Greece) and *batha* (Palestine). Some of the hottest and driest terrain in the Mediterranean is covered with garigue. There are low scattered shrubs, most about 0.5m high, often with patches of stone and rock in between. A large number of herbaceous plants are found including thyme (*Thymus*), rosemary (*Rosmarinus*), sage (*Phlomis*), micromeria (*Micromeria*) and lavender (*Lavandula*), as well as tuberous plants such as crocuses (*Crocus*) and hyacinths (*Hyacinthus*).

On determining a site location, an area of 40x40m (1600m²) was selected by walking for a period of 2 minutes (an arbitrarily chosen time which was used for all sites) into the area. A marker (wooden post) was then placed at that point (here called the *origin point*) which represented the top left corner of the 1600m² site (Section 6.4.1). The method used to select sites was not completely random but, although a limitation, it is a reasonably robust approach because inherent bias is standardized across all sites.

6.3. Sampling periods

The wet period is defined to be from October to the end of May, and the dry period from the end of May to September (Section 3.3). Each of the habitat types (sand, steppe and garigue) was sampled at 20 different sites (Table 6.1).

Ten sites were sampled in the wet period, and ten in the dry period for each habitat type. In this way it was possible to determine whether there were significant differences in the variables measured between the two periods (Section 3.3). Hereafter sites sampled in the wet period are referred to as 'wet sites' and sites sampled in the dry period are referred to as 'dry sites'.

6.4. Sampling layout at the sites

The sampling layout is based on Scheiner *et al.* (2000) and is a *hierarchical nested sample design* (Phillips and Shure, 1990; Palmer and White, 1994; Scheiner *et al.*, 2000 (Figure 6.2); Boyero, 2003 (Figure 6.3); Fleishman *et al.*, 2003)) that allows data to be considered at several levels (Table 6.2), thus allowing the effects of scale to be analyzed (Kluth and Bruelheide, 2004). (See Table 6.3 for comparison of various designs). The data using this method, however, are not strictly independent and this presents problems of pseudoreplication (Hurlbert, 1974; Oksanen, 2001; Hewitt *et al.*, 2007). Using spatial analysis (Section 8.5) may indicate the level of autocorrelation inherent in the data and would be an improvement to this study.

Table 6.2. Possible levels of analysis of variables using focus and grain for the sampling layout used in the present study (see Glossary for definitions of focus and grain).

Focus	Grain					
site	at 1m ² (mean number of species per 20 quadrats)					
	at 5m ² (mean number of species per 4 plots)					
	at 20m ² (total number of species in all 20 quadrats)					
plot	at 1m ² (mean number of species per 5 quadrats)					
	at 5m ² (total number of species in all 5 quadrats)					
quadrats	lm ²					

Table 6.3. Examples of nested sampling designs that use several levels of scale for data analyses for comparison to the design from the present study that is conceptually based on Scheiner *et al.* (2000). See text for further details.

Level	Number of each level	Taxa in study	Total samples in study	Source
Landscape Community Field Quadrat	3 3 per landscape 5 per community 10 per field	Hypothetical	450	Scheiner et al., 2000
Basin Segment Riffle Section Sample	2 3 per basin 3 per segment 3 per riffle 3 per section	Macroinvertebrates	162	Boyero, 2003
Landscape Mountain range Canyon	1 3 5 in 2 ranges; 6 in 1 range 25 in 1 segment, 31 in 1 segment, 28 in 1 segment	Butterflies and birds	448	Fleishman et al., 2003
Habitat type Site Plot Quadrat	3 10 per habitat type 4 per site 5 per plot	Land molluscs	1200	This study

Figure 6.2. The method of Scheiner *et al.* (2000). There are three landscapes (1-3) each with three communities. Within each community there are five fields, each field contains ten quadrats.

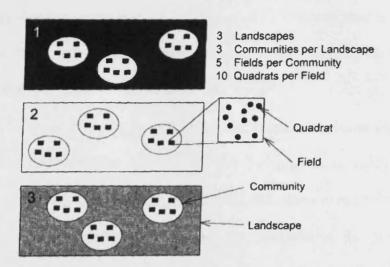
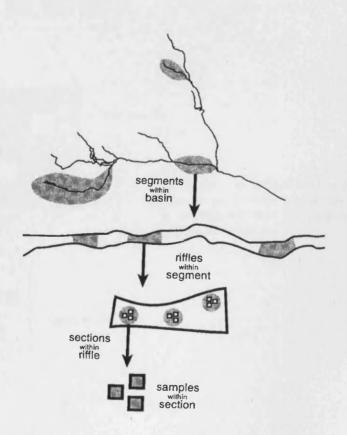


Figure 6.3. The method of Boyero (2003) in which macroinvertebrates were studied from two basins, each contains three segments with three riffles per segment. Each riffle contains three sections, with three samples per section.



6.4.1. Geometry of the sites and selection of the plots and quadrats at the sites

A stratified design (Southwood, 1978; Bart *et al.*, 1998) was used at each of the 1600m^2 sites to select the positions of four plots, each of 5x5m (25m^2). Stratification was used to ensure maximal spread of the plots at the sites by randomly assigning one plot in each of the four blocks, this being the stratum of the stratified design (Figure 6.4). In each plot five quadrats of 1x1m (1m^2) were randomly selected (Oekland, 1929; McIntosh, 1985; Perry *et al.*, 1999). For each site a sequence was generated such that the positions of the plots, and the quadrats in the plots were established before arriving at the site (Figure 6.5).

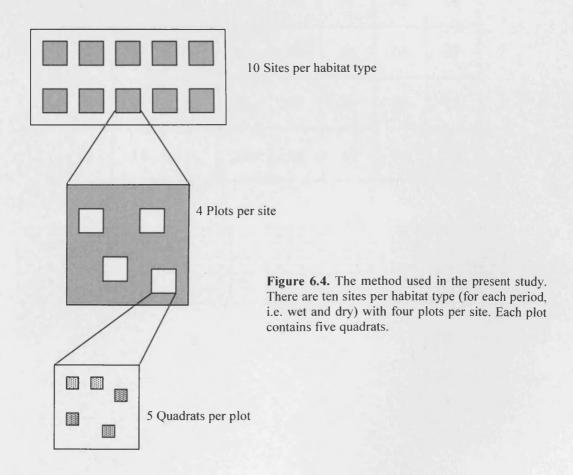


Figure 6.5. Layout of grids for sampling Habitat Structure Sites using a stratified design. The main grid represents the 1600m^2 site divided into 64 possible 25m^2 plots (numbered 00 to 15 for each of the four blocks). Four smaller grids (a. to d.) represent the four selected plots from the main grid. Each plot is divided into 25 quadrats each 1m^2 (numbered 00 to 24).

00	01	02	03	00	01	02	03
04	05	06	07	04	05	06	07
08	09	10	11	08	09	10	11
12	13	14	15	12	13	14	15
00	01	02	03	00	01	02	03
04	05	06	07	04	05	06	07
08	09	10	11	08	09	10	11
12	13	14	15	12	13	14	15

											_									
00	01	02	03	04		00	01	02	03	04		00	01	02	03	04	00	01	02	0
05	06	07	08	09		05	06	07	08	09		05	06	07	08	09	05	06	07	0
10	11	12	13	14		10	11	12	13	14		10	11	12	13	14	10	11	12	1
15	16	17	18	19		15	16	17	18	19		15	16	17	18	19	15	16	17	1
20	21	22	23	24		20	21	22	23	24		20	21	22	23	24	20	21	22	2
					•															

a b c d

Randomness requires that each potential sample unit has an equal chance of being included in the sample, and assigning each potential unit a number and then choosing which units to sample using random numbers is a commonly used method to do this (Greenwood, 1996). Because random number-generating algorithms in computer programs are often not strictly random (Sokal and Rohlf, 1995), the numbers were obtained using a die and random number tables (Kirkwood, 1988; Greenwood, 1996; Bart *et al.*, 1998); the tables used were those from Bliss (1967). The method has these steps:

- 1. A grid is constructed; one for each of the four blocks of the site plan, and one for each of the plots in each block.
- 2. The die is thrown to give the first number that will be the column to be used in the random number table.
- 3. The die is thrown again to give the second number that will be the row to be used in the random number table.
- 4. Steps 2. and 3. provide the section of the random number table to be used, this is also known as the entry point in the table of random numbers and should be different each time that the table is used (Greenwood, 1996).
- 5. The die is thrown again to give the third number that is the column in the section of the random number table.
- 6. The die is thrown again to give the fourth number that is the row in the section of the random number table.

For the selection of positions for plots and quadrats to be used, any positions that were duplicated were rejected and another position found (Table 6.4) (Kirkwood, 1988; Greenwood, 1996).

Table 6.4. Random number sequences for the first ten Habitat Structure Sites showing the plot identities and the quadrat identities for each plot. See text for details of the method used to derive the plot and quadrat identities, and Appendix 7 for sequences for all 60 sites.

Quadrats in:

		Quadrates in:								
Site/ Sequence	Plot ID	Plot a	Plot b	Plot c	Plot d					
1	06,12,10,05	05,12,17,18,24	00,11,13,17,21	01,04,05,15,22	03,08,11,17,19					
2	13,06,14,15	05,06,11,17,21	05,15,20,21,22	01,04,16,17,19	02,08,09,11,15					
3	02,12,08,10	03,14,16,19,23	01,05,16,19,22	03,10,11,20,23	01,04,11,16,24					
4	00,13,07,14	08,09,11,15,21	02,04,10,12,13	02,06,07,16,21	14,15,18,20,21					
5	15,08,06,11	03,07,09,11,24	05,08,09,13,20	03,09,14,19,21	01,04,11,12,23					
6	03,04,08,15	00,07,15,18,20	00,06,15,16,20	02,12,14,17,21	02,12,17,21,24					
7	03,14,06,04	04,08,14,18,21	02,06,09,14,20	05,08,10,17,23	03,10,14,18,21					
8	05,03,13,07	05,11,16,18,21	03,08,14,15,18	02,09,12,14,19	03,07,10,14,17					
9	00,14,07,05	11,14,17,20,21	01,02,06,12,24	03,12,15,17,20	07,08,13,16,21					
10	05,05,07,12	00,03,12,20,21	06,12,14,17,19	03,06,07,13,15	01,07,11,17,22					

6.4.2. Layout of the plots and quadrats at the sites

A wooden post was placed at the top left corner of each site (the origin point, Section 6.2). The linear distance horizontally to the right, and the perpendicular distance below this point correspond to x and y axes from which any coordinate in the grid may be found. The positions of plots were then located by measuring with a metre ruler along the axes (these positions being determined by the random assignment method, Section 6.4.1). The ruler was kept horizontal during measurements by using a spirit level; this removed the possibility of inaccurate distance measurement. The same technique, but now applied to the distances corresponding to the axes of each of the plots in turn, was used to locate the positions of the quadrats in each plot (these positions were also determined by the random assignment method; see above).

Instead of delineating the entire site with rope or string, a metre ruler was used to measure distances from the origin point. To do the former would

have involved a prohibitive amount of time, and would also have presented problems because of surface topography and the presence of obstacles, such as woody shrubs and herbaceous plants. Furthermore, a metre ruler can be placed in between the stems of shrubs to measure distances whereas this is more difficult with a rope or string. The assumption was that any possible inaccuracies in the measurement technique would be consistent at all the sites and thus be standardized.

An aluminium 1m² quadrat was used. This quadrat was designed to be dismantled easily (by using a bolt and wingnut at each of the corners) allowing the quadrat to be placed at ground level even when components of the vegetation (e.g. shrubs) covered areas larger than the quadrat.

6.5. Sampling the quadrats

A pre-determined protocol was followed at each quadrat to provide standardization of data collection at all sites:

- 1. The assessment of vegetational cover for each of the pre-defined vegetation layers (Table 6.5) was carried out by placing a 1m ruler vertically at the top left corner and bottom right corner of the quadrat, then holding a 1m pole across the two rulers corresponding to the height levels of each layer. The vegetation cover was visually assessed at the pre-defined vegetation layers (Section 6.7). In cases where the vegetation was greater than 1m high, an additional metre ruler was placed on top of the first ruler to provide a measureable distance of two metres.
- 2. A thorough search of all vegetation from, but not including, Vegetation

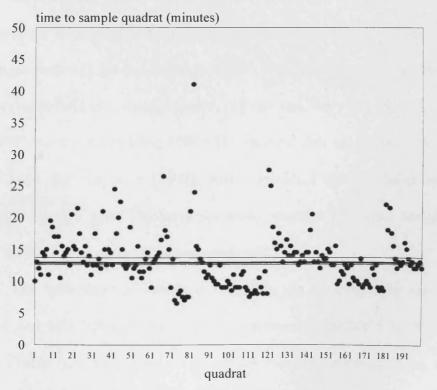
 Layer 2 (see Table 6.5 for vegetation layer classes) upwards for all land

molluscs was carried out (molluscs were identified as described in Section 3.6). The locations of the molluscs in the vegetation (e.g. on annual stem, herbaceous leaf etc. see Appendix 8 for details), as well as the height of these locations (measured from ground level with a metre ruler, to the nearest 0.5cm), were recorded (these data are not used in this study but will be used in future studies). To allow complete vegetation assessment prior to any disturbance this was done before assessing cover of rocks and other variables on the ground, and before the search for species on the ground (and under rocks). Once completed, the ground level features, such as rock cover and soil cover (Section 6.7) were assessed.

- 3. Plant stem width, 5cm from ground level, was measured using calipers and recorded to the nearest 0.1mm. To minimize bias in the selection of plants for measuring, two stems of each plant type (Section 6.8) were chosen from the four corners and the centre of the quadrat (for a total of ten measures per plant type). In cases where these regions of the quadrat had no, or insufficient plant stems, the position nearest any of the points was used in each case.
- 4. The ground level and Vegetation Layer 2 were thoroughly searched for molluscs. The procedures described in 2. and 3. above, as well as the search for molluscs from the ground level, often resulted in the upper layers of vegetation being disturbed, and rocks and other ground level features being moved. In all cases, however, rocks, plants etc. were returned to their original positions as far as was possible to reduce any damage that the sampling may have done.

The quadrat sampling protocol involved the systematic and thorough search for molluscs on the vegetation, and under rocks and other ground-level features, as well as the recording of the environmental variables (Section 6.6). This type of sampling is termed *dissection sampling* to describe the detailed examination and analysis of the quadrat components, and to highlight the differences between this method and less thorough search and data recording techniques sometimes used in studies. The thoroughness of the method is reflected in the time required to sample a quadrat (Figure 6.6). The protocol also allows quadrats to be sampled to the same level of detail, regardless of habitat heterogeneity and complexity.

Figure 6.6. The time in minutes (measured to the nearest 0.5 minute) required to sample 200 quadrats from 20 sites (quadrats were randomly selected from 400 quadrats from sand, steppe and garigue habitat types). The Figure shows the position of the mean (bold line) and 95% confidence intervals of the mean (fine lines). (The outlier value is from a quadrat with exceptionally dense vegetation).



mean: 13.31; min: 6.5; max: 41.0; 95% Confidence Interval for mean, lower: 12.70; upper: 13.91; sd: $4.31\,$

6.6. The environmental variables

It is not possible to know all the variables that are important in determining numbers of species, abundances, distribution and community structure; and an efficient policy for any detailed study is to include as many as practicable (Table 6.5) based on knowledge of the ecology of the taxa under investigation and the questions being asked (Barnard *et al.*, 2001). The need to include environmental variables in ecological studies was highlighted by Elton and Miller (1954) in their influential paper that advocated a system for classifying habitats using structural characters. Dunson and Travis (1991) argued that environmental variables must be included as possible controlling variables in any complete study, and Bishop (1977), referring specifically to land mollusc ecology, stated that the systematic collecting of habitat factors is essential.

In this study *environmental variable* is defined as any variable that is measured for its possible effects on the numbers, abundances and distributions of species at sites (Lepš and Šmilauer, 2003). The definition thus includes biotic and environmental (i.e. abiotic) factors (Clarke and Warwick, 1994; Lincoln *et al.*, 1998; Jones and Reynolds, 1996). The species' data are the primary data set *sensu* Lepš and Šmilauer (2003), with individual species being response variables (Section 3.4). The environmental variables measured are given in Table 6.5, including notes on measurement and scoring.

The environmental variables constitute the Heterogeneity axis of the McCoy and bell (1991) model of habitat structure (Section 5.3). Vegetation layers (Table 6.5) are treated as individual variables although these are not strictly discrete (the existence of vegetation layer 5, for example, is dependent on the existence of layers below this).

Table 6.5. The environmental variables showing measurement/scoring criteria, and notes, (GPS=Global Positioning System, %c=percentage cover).

Variable name			leasureme		3	Die 2	Notes		
Altitude	Metres	above M	ean Sea Le	vel			Using altimeter		
Latitude	Degrees						Using GPS		
Longitude	Degrees						Using GPS		
			12			11000	1: loam, 2: sand, 3: clay,		
Nature of soil	Percenta	age cover	r			100	4: gravel. Visual		
			estimation ¹						
							Size: 1: <10mm, 2: 10-		
						1.0	25mm, 3: 25-50mm, 4:		
Nature of leaf litter	Percenta	age cove	7				>50mm. Visual		
							estimation ¹		
THE RESERVE OF THE PARTY OF THE		1 35 4			-2014	100	1: angular, 2:		
							intermediate, 3:		
Shingle (2-10mm)	Percent	age cove	r				rounded. Visual		
						is Ibi	estimation ¹		
Stones (10-50mm)	Percent	age cove	r				Visual estimation. 1,2		
Rocks	-	age cove					Visual estimation. 1,2		
T.COR.S				-			Size: 1: <10mm, 2:10-		
Rubble	Percent	age cove	r				50mm, 3: >50mm.		
	1 Crociiti	-50 0010					Visual estimation ¹		
	11111	William I	WALL TO SERVICE STREET				Size: 1: <10mm, 2:10-		
Logs	Percent	age cove	r				50mm, 3: >50mm.		
2083	1 Crecilla	age cove				-33	Visual estimation ¹		
Wood (excluding logs)	Percent	age cove	r				Visual estimation		
Refuse: card/paper		age cove					Visual estimation		
Refuse: plastic							Visual estimation		
		age cove							
Refuse: glass		age cove					Visual estimation		
Refuse: other	Percent	age cove	r				Visual estimation		
							Size: 1: <10mm, 2:10-		
Bryophytes	Percent	age cove	r				50mm, 3: >50mm.		
							Visual estimation ¹		
Lichens	Percent	age cove	r				Visual estimation		
			17421				Using 1 Molar HCl.		
			tion, 2: no				Positive reaction is		
HCl reaction of rock			al cases, 4				indicated by the		
Tierreaction of fock			cases, 5: p		nd no re	action-	liberation of gas from		
	more no	reaction	n cases, 6:	no rocks			the rock on contact with		
				1 12 1			HCl ³		
Vegetation layer (cm from	Green	Dry	Annual	Herb-	Shrub	Tree			
ground)	grass	grass		aceous					
					100				
1 (0-10)	(%c)	(%c)	(%c)	(%c)	(%c)	(%c)	Visual estimation		
2 (10-20)	(%c)	(%c)	(0/0)				Visual estimation		
	(,00)		(%c)	(%c)	(%c)	(%c)	Visual estimation Visual estimation		
	(%c)	(%c)	(%c)	(%c)	(%c)	(%c)	Visual estimation Visual estimation		
3 (20-30)							Visual estimation		
3 (20-30) 4 (30-40)	(%c)	(%c)	(%c) (%c)	(%c)	(%c)	(%c)	Visual estimation Visual estimation		
3 (20-30) 4 (30-40) 5 (40-50)	(%c) (%c) (%c)	(%c) (%c) (%c)	(%c) (%c) (%c)	(%c) (%c) (%c)	(%c) (%c) (%c)	(%c) (%c) (%c)	Visual estimation Visual estimation Visual estimation Visual estimation		
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Data used only as %c in this study.

2 See Appendix 9 for characterization of shingle, stones and rocks.

3 Data not used in this study.

6.7. Visual estimates of percentage cover

A large number of the variables used in this study were measured using visual estimates of percentage cover, a technique widely used in ecology studies (Brower et al., 1989; Cox, 1990; Johansson and Ehrlén, 2003; Lepš and Šmilauer, 2003; Casado et al., 2004), although mostly to measure plant cover. In the early 1920s, L.G. Ramensky defined vegetation abundance as: 'a specific area of horizontal projection of ground shoots', a definition that later came to be called cover and which Greig-Smith (1983) defined as: 'the proportion of ground occupied by a perpendicular projection onto it of the aerial parts of individuals of the species' (see McIntosh (1985) for discussion).

Cover is usually considered as the area of a quadrat occupied by species when viewed from above (Kent and Coker, 1992). This can be extended to include cover in vegetation layers recorded separately (Bullock, 1996). Several measurement scales are used for recording cover (Goldsmith *et al.*, 1986; Kent and Coker, 1992); two of the most popular are the Braun-Blanquet and Domin scales (Table 6.6). Cover as percentage (as in this study) is, however, sometimes used and is preferable for some statistical analyses (Dytham, 1999). Cover was assessed to the nearest 5%; above this resolution, visual assessments are probably inaccurate. When cover was very low a value of 1% cover was assigned and this generally applied to very scanty cover, or the presence of a few plant individuals or a few stones etc. This measurement is comparable to the + value used in the Braun-Blanquet and Domin scales (Table 6.6).

Table 6.6. The Braun-Blanquet and Domin scales: two widely used scales for the measurement of percentage cover of vegetation (from Kent and Coker, 1992).

value	Braun-Blanquet	Domin					
+	Less than 1% cover	A single individual. No measureable cover.					
1	1-5% cover	1-2 individuals. No measureable cover. Individuals with normal vigour.					
2	6-25% cover	Several individuals but less than 1% cover.					
3	26-50% cover	1-4% cover					
4	51-75% cover	4-10% cover					
5	76-100 % cover	11-25% cover					
6		26-33% cover					
7		34-50% cover					
8		51-75% cover					
9		76-90% cover					
10		91-100% cover					

Casado *et al.* (2004) assessed herbaceous plant richness and vegetation cover in Spain and Portugal, and used visually calculated cover of vegetation. Smartt *et al.* (1974) found that measures of cover assessed subjectively were a good approximation to more accurate, and time intensive, methods. Inaccuracies that may result because of the subjectivity inherent in these methods (Greig-Smith, 1983; Bullock, 1996) are expected to be consistent with each recorder. Bias in estimation may therefore be expected to be similar across sites. Many land mollusc ecology studies have used estimation methods for assessing vegetation cover (Dillon 1980; Tattersfield 1996; Barker and Mayhill, 1999; Craze and Lace, 2000; Hylander *et al.*, 2005).

6.8. Characterization of plant types

Plants were categorized into six types based on Polunin and Walters (1985), Polunin and Huxley (1987), Polunin and Smythies (1988) and Bello *et al.* (2005). In this way the vegetation could be sampled adequately without the need to identify each plant species (which would have been prohibitive), whilst providing information on the vegetation architecture. The six types are:

1. Green grass: For example species of Agropyron, Lagurus, Stipa, Cynodon and Piptatherum.

- 2. Dry grass: This type contains the same species as green grass but as dry plants. Green and dry grasses were measured separately because grasses often compose a large proportion of the total vegetation cover in some habitats and the proportions of each vary widely between the wet and dry seasons.
- 3. Annual: Many species including *Plantago*, *Andryala*, *Chrysanthemum*, *Linum* and *Trifolium*.
- 4. Herbaceous: These are generally non-woody plants with sappy stems that often die back at the end of the growing period. Examples are *Malva, Lavatera, Erodium, Dianthus* and *Echium*.
- 5. Shrub: These are generally woody plants that can attain heights of about 2m, but normally less than 1m in garigue habitats; for example, Ulex, Genista, Phlomis, Cistus and Pistacia.
- 6. Tree: Woody plants mostly over 2m in height, sometimes present as scattered individuals in sand, steppe and garigue habitats. Examples are *Pinus, Ficus, Quercus, Osyris* and *Ceratonia*.

6.9. Data analysis

6.9.1. Diversity analysis

6.9.1.1. The number of species

This is a measure of the number of species at each of the sites; specimens were identified to species level (Section 3.6). This measure is also known as species richness (McIntosh, 1967) and is the oldest measure of biological diversity (Magurran, 2004).

6.9.1.2. Abundances of the species

The numbers of individuals of each of the species at each of the sites were recorded to provide the abundance of each species. The term abundance is synonymous with density when (as in this study) the unit of area or volume from which the species are counted is known (Krebs, 1985; Bullock, 1996).

6.9.1.3. Diversity

There is considerable debate about how species diversity should be measured and some indices make assumptions that are sometimes not met by the species data that they are used for (Section 3.7.1.3). In this study two indices of species diversity were used: Simpson's index (*Ds*) and the Shannon index (*H'*) (Magurran, 1988, 2004). These two indices are commonly used in ecological studies and allow comparison of data from the present study with those from other studies.

6.9.1.3.1. Simpson's index

This is calculated using $D = \frac{\sum n_i(n_i - 1)}{N(N - 1)}$ where n_i is the number of individuals of the *i*th species and N is the total number of individuals. The reciprocal form (Ds) is used to ensure that the value of the index increases with increasing diversity; this is given by $Ds = \frac{1}{D} = \frac{N(N-1)}{\sum n_i(n_i - 1)}$ (Magurran, 2004).

6.9.1.3.2. Shannon index

This is calculated using $H' = -\Sigma p_i \ln p_i$ where p_i , the proportional abundance of the *i*th species = (n_i/N) . Base 2 logs were used for calculating the Shannon index (Magurran, 2004). Indices were derived from the species abundances matrix using the DIVERSE routine in PRIMER (Plymouth Routines in Multivariate Ecological Research; Carr, 1991, 1997; Clarke and Warwick, 1994). To assess

all of the measures described (Sections 6.9.1.1. to 6.9.1.3) the mean, 95% confidence intervals (CI), minimum, maximum and range were used. CI were used instead of standard error (SE) of the mean following Dytham (2003) who states that CI is preferred over SE because the latter is useful only if the sample size is known. This criterion is almost never met with number of species and species abundances data.

6.9.2. Tests of Hypotheses about habitat structure

Sixteen hypotheses were tested (Table 6.7). These are outlined below.

H_1 : The higher the heterogeneity, the more species are present

The greater the number of types of habitat structure (i.e. heterogeneity) present, the more variety of shelter and micro-habitats that are expected to be available to land molluscs, allowing the coexistence of more species than where heterogeneity is lower.

H_2 : The higher the heterogeneity, the higher the abundances of species

The greater the number of types of habitat structure (i.e. heterogeneity) present, the more variety of shelter and micro-habitats that are expected to be available to land molluscs, allowing higher abundances of land molluscs than where heterogeneity is lower. Species abundance data were \log_{x+1} transformed.

H_3 : The higher the complexity, the more species are present

The greater the quantity of habitat structure (i.e. complexity) present, the more that is expected to be available to land molluscs, allowing the coexistence of more species than where complexity is lower.

Table 6.7. Summary of the hypotheses tested (see Table 7.19 for results of testing these hypotheses).

Hypothesis number	Description	Analyses
H_1	The higher the heterogeneity, the more species present	Spearman's correlation of heterogeneity with number of species
H_2	The higher the heterogeneity, the higher the abundances of species	Spearman's correlation of heterogeneity with abundances of species
H_3	The higher the complexity, the more species present	Spearman's correlation of complexity with number of species
H_4	The higher the complexity, the higher the abundances of species	Spearman's correlation of complexity with abundances of species
H ₅	Some types of heterogeneity affect number of species independently of total complexity	Partial correlations between variable pairs, whilst holding total complexity constant
H_6	Some types of heterogeneity affect abundances of species independently of total complexity	Partial correlations between variable pairs, whilst holding total complexity constant
H_7	The number of species increases as spatial scale increases	ANOVA
H_8	The abundances of species increases as spatial scale increases	ANOVA
H ₉	There is more variation in heterogeneity in some habitat types than in others	Coefficient of Variation (CV) of heterogeneity
H_{10}	There is more variation in complexity in some habitat types than in others	Coefficient of Variation (CV) o complexity*
H_{II}	Heterogeneity differs between the habitat types	ANOVA
H ₁₂	Complexity differs between the habitat types	ANOVA
H_{13}	Heterogeneity differs between the wet and dry periods at each habitat type	ANOVA
H ₁₄	Complexity differs between the wet and dry periods at each habitat type	ANOVA
H_{15}	Heterogeneity differs between the wet and dry periods between the habitat types	ANOVA
H ₁₆	Complexity differs between the wet and dry periods between the habitat types	ANOVA

^{*}The CV is used to assess variation of heterogeneity and complexity from sites. The analysis does not enable significance testing and so, strictly, this is not a formal statistical testing of the hypotheses. The decision to accept/reject the hypotheses is based on the values of CV for the habitat types (see Tables 7.1 to 7.8, and 7.13 to 7.15, and, text for further details).

H_4 : The higher the complexity, the higher the abundances of species

The greater the quantity of habitat structure (i.e. complexity) present, the more that is expected to be available to land molluscs, allowing higher abundances of land molluscs than where complexity is lower. Species abundance data were \log_{x+1} transformed.

H_5 : Some types of heterogeneity affect the number of species independently of total complexity

Some types of structure may be more important in affecting number of species than others. For example, rocks (that provide shelter from desiccation and predation) may be more important than soil. The presence of some types of structure may thus affect the number of species of land molluscs independently of the total quantity of structure (i.e. total complexity). Data were \log_{x+1} transformed (Krebs, 1985; Clarke and Warwick, 1994).

H_6 : Some types of heterogeneity affect the abundances of species independently of total complexity

Some types of structure may be more important in affecting the abundances of species than others. The presence of some types of structure may thus affect the abundances of species of land molluscs independently of the total quantity of structure (i.e. total complexity). Data were \log_{x+1} transformed.

H_7 and H_8 : The number and abundances of species increases as spatial scale increases

It is expected that estimates of the number of species (H_7) and abundances (H_8) of land molluscs will increase with increasing scale (for example, from 1m^2 to 5m^2 to 20m^2). ANOVA was carried out to test these hypotheses.

 H_9 and H_{10} : There is more variation in heterogeneity and complexity in some habitats than in others

Some habitats are more heterogeneous than others and variation in heterogeneity (as types of habitat structure) (H_9), and complexity (as quantity of habitat structure) (H_{I0}) are expected to vary more in some habitats than others.

 H_{11} and H_{12} : Heterogeneity and complexity differ between the habitat types

 H_{13} and H_{14} : Heterogeneity and complexity differ between the wet and dry periods at each habitat type

 H_{15} and H_{16} : Heterogeneity and complexity differ between the wet and dry periods between the habitat types

6.9.3. Habitat diversity

Spearman's rank correlation of the number of species, abundances, species diversity and heterogeneity, complexity and habitat diversity were carried out at three levels of scale (1m², 5m² and 20m²). Habitat diversity was calculated from the environmental variables (Section 6.6) using Shannon (log₂) and Simpson's diversity (Magurran, 1988) using PRIMER. In these calculations heterogeneity (types of habitat structure) is analogous to number of species, and complexity (quantity of habitat structure) is analogous to species abundances (see Magurran, 1988 for discussion). The efficacy of habitat structure indices was judged on the criterion that these indices provide the same results as *both* heterogeneity and complexity for the sites.

6.9.4. Relationships across scale: correlations

Spearman's rank correlation of the number of species, abundances, species diversity, and heterogeneity and complexity were carried out at three levels of scale (1m², 5m² and 20m²) (Section 6.9.3).

6.9.5. Variance in vegetation: plant stem widths

Variance in the plant types (Section 6.8) was assessed using the means and standard deviations of the stem widths.

6.9.6. Presence/absence of molluscs in quadrats, plots and sites

The numbers of quadrats, plots and sites at which molluscs were present and absent were quantified.

6.9.7 Species estimators

In Part One sampling methods were designed to record as many species as possible at the sites (Section 3.5). Direct search and soil sampling were carried out using a specific time period and volume of soil previously shown to be adequate for Mediterranean habitat types (Sections 3.5.1 and 3.5.2). In Part Two the aim of sampling was to record every individual in each quadrat. This was carried out using dissection sampling (Section 6.5) that resulted in disruption and disturbance of the habitat components. This type of sampling, that can be viewed as a form of 'habitat destruction', is possibly the only way all species can be found at a location (Cameron and Pokryszko, 2005). Sampling species in this way allows the recording of absolute numbers of species (Magurran, 2004).

To assess the efficacy of this approach, nonparametric species estimators were used (Cameron and Pokryszko, 2005). These measures are not based on the parameter of a previously fitted species abundance model (Magurran, 2004; Hortal *et al.*, 2006), and include the Chao 1, Chao 2, Bootstrap and Abundance-based Coverage Estimator (ACE) that are reviewed and assessed by Butler and Chazdon (1998), Chazdon *et al.* (1998), Melo and Froehlich (2001), Magurran (2004), O'Hara (2005), and Walther and Moore (2005).

Nonparametric estimators are a significant advance in diversity measurement (Gotelli and Colwell, 2001; Magurran, 2004; Chao *et al.*, 2005) and the Chao estimators (Chao, 1984; 1987; Chao and Lee, 1992; Chao *et al.*, 1992; 1993) have been used by Cameron and Pokryszko (2004) to assess land mollusc diversity in Polish forests. These two estimators perform well (Hortal *et al.*, 2006), are recommended by Cameron and Pokryszko (2005) for checking sampling efficacy in land mollusc surveys, and are used in this study.

Chao 1 is calculated using $S_{Chao1} = S_{obs} + \frac{F_1^2}{2F_2}$, where $S_{obs} =$ the number of species in the sample, $F_1 =$ the number of observed species represented by a single individual (singletons), and $F_2 =$ the number of observed species represented by two individuals (doubletons) (Magurran, 2004). Chao 2 is calculated using $S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$, where $S_{obs} =$ the number of species in the sample, $Q_1 =$ the number of species that occur in one sample only (unique species), and $Q_2 =$ the number of species that occur in two samples (Magurran, 2004). Chao 1 and Chao 2 calculations were carried out using the program EstimateS (Statistical Estimator of Species Richness and Shared Species from Samples, Colwell, 2004) and 1000 different randomizations of sample order were used. This reduces the effect of sample order by averaging over randomizations (Colwell, 2004).

Chao 1 uses abundance data while Chao 2 uses presence/absence data. The estimate of the number of species produced by Chao 1 is a function of the ratio of singletons and doubletons, and this estimate exceeds the observed number of species by larger amounts as the number of singletons increases

(Colwell, 2004; Magurran, 2004). In addition, the more unique species there are, the less well that Chao 2 performs (Colwell, 2004; Magurran, 2004).

6.9.8. Species accumulation curves

Species accumulation curves were derived for all sites using PRIMER and the quadrat at which an asymptote was attained for each site recorded (assessed visually). This approach is similar to that used in studies with the guppy *Poecilia reticulata* Peters, 1859 (Magurran, 2004; Magurran and Phillip, 2001). The first mathematical description of the relationship between the area sampled and the number of species found was given by Arrhenius (1921). This was based on the number of plant species, and Darlington (1957) described the relationship using reptiles and amphibians.

Species accumulation curves are one of two forms of species-area curves (Gray et al., 2004; Dove and Cribb, 2006; Lyman and Ames, 2007). The first type plots number of species versus area for different areas (such as islands); the second plots number of species versus larger parcels of the same region. Only the latter should be regarded as a species accumulation curve since this depicts the same 'universe' at different intensities (Magurran, 2004). Species rarefaction curves differ from species accumulation curves in that they are plots of the cumulative species richness as a function of the number of sampled individuals (Hurlbert, 1971; Crist and Veech, 2006).

The species accumulation curve is the oldest and best known technique to estimate the level of error in sampling inventories (Loehle *et al.*, 2005; Cameron and Pokryszko, 2005). If an asymptote is attained the inventory may be complete and the sampling effort can be determined (Cameron and

Pokryszko, 2005). Menez (2001) applied this technique to land molluscs and assessed sampling efficacy in Mediterranean habitats (Section 3.5.1).

6.9.9. Transformations

Transformations were carried out on data for two different reasons (Clarke and Warwick, 1994; Sokal and Rohlf, 1995):

- 1. to validate the assumptions for parametric tests (e.g. for ANOVA);
- 2. to weight the contributions of common and rare species in analyses.

Data were analyzed using the Kolmogorov-Smirnov test (K-S) for goodness of fit using the 1 sample K-S routine in SPSS that compares the data with a theoretical normal distribution and computes K-S z. If the distribution of the data is significantly different from normal the significance (2-tailed P) is less than 0.05.

A variety of transformations can be used ranging from a square root transformation to converting the data to presence/absence (Clarke and Warwick, 1994; Legendre and Gallagher, 2001; Section 3.7.2.9). In this study the \log_{x+1} transformation is used for both species data and environmental data (Section 3.7.2.9).

CHAPTER 7. RESULTS AND DISCUSSION

7.1. Results

7.1.1. The numbers of species, abundances and diversity

A total of 55 species were recorded from the 60 sites (see Appendix 10 for data at individual sites, Appendix 3 for systematic species list and Appendix 6 for site photographs). There was a mean number of six species at each site (lower 95% CI: 5.26; upper 95% CI: 6.74) with a mean total species abundance of 358.67 (lower 95% CI: 247.26; upper 95% CI: 470.07), a mean Shannon diversity of 1.443 (lower 95% CI: 1.282; upper 95% CI: 1.603) and a mean Simpson's diversity of 0.516 (lower 95% CI: 0.464; upper 95% CI: 0.568). (Table 7.1, Figure 7.1). There were more species in the wet period at sand and garigue habitats than in the dry period (at the three grain levels), but in the steppe habitat there were more species in the dry period. Combining all sites (wet and dry), the habitat types order from lowest to highest for number of species as: (1) sand, (2) steppe, and (3) garigue. Abundances were higher in the wet period at sand and steppe habitats than in the dry period (at the three grain levels), but abundances were higher in the dry period in garigue. Combining all sites (wet and dry), the habitat types order from lowest to highest for abundances as: (1) steppe, (2) garigue and (3) sand.

Shannon and Simpson's diversity were higher in the wet period at sand and garigue habitats than in the dry period (at the three grain levels), but diversity was higher in the dry period in steppe. Combining all sites (wet and dry), the habitat types order from lowest to highest for diversity as: (1) sand, (2) steppe, (3) garigue.

7.1.2. Tests of hypotheses about habitat structure

H_1 : The higher the heterogeneity the more species that are present

There was a significant positive correlation between heterogeneity and number of species for most habitat types and period combinations (Table 7.2). This suggests that increased heterogeneity is associated with a higher number of species. The association was not significant for dry sand sites, but was significant for wet sand sites (Table 7.2).

H_2 : The higher the heterogeneity, the higher the abundances of species

Correlations between heterogeneity and the abundances of species were not significant for garigue sites nor when data were pooled from all sites (Table 7.3). Increased heterogeneity is therefore not associated with higher abundances of species. The correlations were positive for sand (all sites, wet sites) and steppe (all sites, wet sites, dry sites).

Table 7.1. Mean, standard deviation (sd), minimum (min), maximum (max), range, lower and upper 95% confidence intervals of the mean (CI) for the number of species, abundances, Shannon (\log_2) and Simpson's diversity at all sites, wet sites combined and dry sites combined, and for each of the habitat types (sand, steppe, garigue) for each of the three levels of grain (1m^2 , 5m^2 and 20m^2).

Grain (m²)	n	Mean	sd	min	max	Range	Lower 95% CI	Upper 95% CI
			Numbe	er of specie	es: All sites			
1	1200	1.94	1.549	0	9	9	1.86	2.03
5	240	3.76	2.182	0	13	13	3.49	4.04
20	60	6.00	2.852	2	14	12	5.26	6.74
			Numbe	er of specie	es: Wet site	25		
1	600	2.01	1.633	0	9	9	1.88	2.14
5	120	3.83	2.414	0	13	13	3.39	4.26
20	30	6.37	3.253	3	14	11	5.15	7.58
			Numbe	er of specie	es: Dry site	es		
1	600	1.88	1.458	0	8	8	1.76	1.99
5	120	3.70	1.930	0	10	10	3.35	4.05
20	30	5.63	2.385	2	11	9	4.74	6.52
			Numbe	er of specie	es: SAND	All sites		
1	400	1.95	1.352	0	9	9	1.82	2.08
5	80	3.31	1.776	0	13	13	2.92	3.71
20	20	4.85	2.498	2	14	12	3.68	6.02

Table 7.1 (continued).

Grain (m²)	n	Mean	sd	min	max	Range	Lower 95%	Upper 95%
		C. El Great A.	Nous	C :	CAND I	Wat aid an	CI	CI
1	200	2.08	1.453	()	es: SAND	yei siles	1.87	2.28
5	40	3.43	2.147	0	13	13	2.74	4.11
20	10	5.40	3.098	4	14	10	3.18	7.62
20	10	3.40			es: SAND I		3.10	7.02
1	200	1.83	1.234	0	5	5	1.65	2.00
5	40	3.20	1.324	1	6	5	2.78	3.62
20	10	4.30	1.703	2	7	5	3.08	5.52
20	10	4.50			es: STEPP		3.00	3.32
1	400	1.79	1.496	0	7	7	1.64	1.93
5	80	3.66	2.267	0	9	9	3.16	4.17
20	20	6.10	2.447	2	10	8	4.95	7.25
20	20	0.10				E Wet sites	4.75	1.23
1	200	1.75	1.432	0	7	7	1.55	1.94
5	40	3.58	2.297	0	8	8	2.84	4.31
20	10	6.30	2.452	3	9	6	4.55	8.05
20	10	0.50				E Dry sites	1.55	0.03
1	200	1.83	1.560	0	7	7	1.61	2.05
5	40	3.75	2.263	0	9	9	3.03	4.47
20	10	5.90	2.558	2	10	8	4.07	7.73
		3.70				UE All site		1 7.73
1	400	2.09	1.760	0	8	8	1.92	2.27
5	80	4.31	2.363	1	10	9	3.79	4.84
20	20	7.05	3.236	3	14	11	5.54	8.56
						UE Wet sit		1 0.00
1	200	2.21	1.938	0	8	8	1.94	2.48
5	40	4.47	2.689	1	10	9	3.62	5.33
20	10	7.40	4.033	3	14	11	4.51	10.29
			Numbe	er of speci	es: GARIG	UE Dry sit	es	1
1	200	1.98	1.558	0	8	8	1.76	2.19
5	40	4.15	2.007	1	10	9	3.51	4.79
20	10	6.70	2.359	3	11	8	5.01	8.39
		V-17-	Species	abundan	ces: All sit	es		
1	1200	17.73	30.041	0	373	373	16.03	19.44
5	240	90.20	130.025	0	711	711	73.66	106.7
20	60	358.67	431.257	7	2035	2028	247.26	470.0
		200.07			ces: Wet si		2.7.20	1,70.0
1	600	20.76	33.091	00	271	271	18.10	23.41
5	120	104.37	147.091	0	705	705	77.78	130.9
20	30	414.40	514.890	7	2035	2028	222.14	606.60
					ces: Dry si			200.00
1	600	14.71	26.328	0	373	373	12.60	16.82
5	120	76.03	109.152	0	711	711	56.29	95.76
20	30	302.93	326.864	13	1287	1274	180.88	424.99
5-11					ces: SANL			
1	400	26.45	34.149	0	170	170	23.09	29.80
5	80	133.76	148.608	0	674	674	100.69	166.83
20	20	528.65	529.245	20	2035	2015	280.96	776.34
					ces: SAND		200,70	770.5
1	200	33.98	40.792	0	170	170	28.89	39.66
5	40	171.35	180.995	0	674	674	113.47	229.23
20	10	678.90	666.761	34	2035	2001	201.93	1155.8

Table 7.1 (continued).

Grain (m ²)	n	Mean	sd	min	max	Range	Lower 95%	Upper 95%
(m)							CI	CI
		4 4 1 1	Specie	s abundan	ces: SAND	Dry sites		
1	200	18.92	23.670	0	134	134	15.62	22.22
5	40	96.18	95.278	1	388	387	65.70	126.6
20	10	378.40	310.785	20	923	903	156.08	600.7
			Specie	s abundan	ces: STEP	PE All sites	S	
1	400	12.98	24.273	0	271	271	10.59	15.36
5	80	64.79	105.386	0	705	705	41.34	88.24
20	20	259.15	348.280	7	1269	1262	96.15	422.1
			Specie	s abundan	ces: STEP	PE Wet site	es	
1	200	18.40	31.926	0	271	271	13.94	22.85
5	40	91.93	139.36	0	705	705	47.35	136.5
20	10	367.70	464.579	7	1269	1262	35.36	700.0
	1, 11 77		Specie	s abundan	ces: STEP.	PE Dry site	es	ED ED N
1	200	7.56	10.154	0	82	82	6.14	8.98
5	40	37.65	39.535	0	183	183	25.01	50.29
20	10	150.60	118.566	0	319	306	65.78	235.4
			Specie	s abundan	ces: GARI	GUE All si		-
1	400	13.78	29.019	0	373	373	10.93	16.63
5	80	72.04	122.667	1	711	710	44.74	99.34
20	20	288.20	360.636	10	1287	1277	119.42	456.9
			Specie	s abundan	ces: GARI	GUE Wet s	ites	
1	200	9.90	17.692	0	159	159	7.43	12.36
5	40	49.83	77.608	1	411	410	25.0	74.65
20	10	196.60	246.943	10	751	741	19.95	373.2
			Specie	s abundan	ces: GARI	GUE Dry s		
1	200	17.66	36.676	0	373	373	12.55	22.77
5	40	94.25	153.117	2	711	709	45.28	143.2
20	10	379.80	441.521	21	1287	1266	63.96	695.6
			Shann	on diversit	y: All sites			
1	1200	0.6368	0.6565	0	2.9477	2.9477	0.5996	0.674
5	240	1.0847	0.6808	0	2.8758	2.8758	0.9982	1.171
20	60	1.4427	0.6220	0.4690	2.7305	2.2615	1.2820	1.603
20	00	1.4427			y: Wet sites		1.2020	1.0034
1	600	0.6847	0.6630	0	2.9477	2.9477	0.6316	0.7379
5	120	1.1144	0.7034	0	2.8758	2.8758	0.9873	1.241:
20	30	1.5230	0.6026	0.6185	2.7305	2.1120	1.2980	1.7480
20	30	1.3230			y: Dry sites		1.2700	1./400
1	600	0.5889	0.6470	0	2.6258	2.6258	0.5370	0.6408
5	120	1.0551	0.6590	0	2.4278	2.4278	0.9360	1.1742
20	30	1.3625	0.6408	0.4690	2.4403	1.9713	1.1232	
_20	30	1.3023			y: SAND A		1.1232	1.6017
1	400	0.6169	0.5671	0	2.8285	2.8285	0.5612	0.6725
5	80	0.8931	0.5435	0	2.4165	2.4165	0.3612	0.6727
20	20	1.3499	0.3433	0.4690	2.5274	2.0584	0.7722	1.0141
20	20	1.5499			y: SAND W		0.9090	1.3670
1	200	0.6974		on aiversii 0	2.8285		0.6044	0.7707
1	200	0.6874	0.5952	0		2.8285	0.6044	0.7705
5	40	0.9251	0.6077		2.4165	2.4165	0.7304	1.1194
20	10	1.3178	0.5446	0.6185	2.5274	1.9089	0.9282	1.7073
1	200	05464			v: SAND D		0.450 - 1	0.75
1	200	0.5464	0.5299	0	1.9621	1.9621	0.4725	0.6203
5	40	0.8613	0.4764	0 1600	1.9219	1.9219	0.7089	1.0137
20	10	0.9618	0.3791	0.4690	1.5903	1.1214	0.6906	1.2330

Table 7.1 (continued).

Grain (m²)	n	Mean	sd	min	max	Range	Lower 95% CI	Upper 95% CI
			Shann	on diversit	y: STEPPE	All sites		
1	400	0.6067	0.6487	0	2.6258	2.6258	0.5429	0.6704
5	80	1.0806	0.6697	0	2.4278	2.4278	0.9316	1.2296
20	20	1.5216	0.5272	0.6194	2.4403	1.8209	1.2749	1.7684
		142 15 44	Shann	on diversit	y: STEPPE	Wet sites		
1	200	0.5900	0.5731	0	2.3098	2.3098	0.5101	0.6700
5	40	1.0438	0.5923	0	2.2480	2.2480	0.8543	1.2332
20	10	1.4380	0.3842	0.9858	2.1385	1.1526	1.1631	1.7128
				on diversit	y: STEPPE			
1	200	0.6233	0.7174	0	2.6258	2.6258	0.5232	0.723
5	40	1.1174	0.7449	0	2.4278	2.4278	0.8792	1.355
20	10	1.4999	0.7752	0.6194	2.7305	2.1111	0.9453	2.054
				on diversit	y: GARIGU			
1	400	0.6868	0.7410	0	2.9477	2.9477	0.6140	0.7560
5	80	1.2804	0.7630	0	2.8758	2.8758	1.1106	1.4502
20	20	1.6668	0.7250	0.4907	2.7305	2.2398	1.3275	2.0061
					y: GARIGU			
1	200	0.7767	0.7891	0	2.9477	2.9477	0.6666	0.8867
5	40	1.3743	0.8235	0	2.8758	2.8758	1.1109	1.6377
20	10	1.8188	0.7600	0.6651	2.7305	2.0654	1.2697	2.3569
		T			y: GARIGU			201
1	200	0.5970	0.6796	0	2.2464	2.2464	0.5022	0.6917
5	40	1.1866	1.6950	0	2.2780	2.2780	0.9643	1.4089
20	10	1.5202	0.6959	0.4907	2.3060	1.8153	1.0224	2.0180
					ity: All sites			
1	1200	0.3069	0.3180	0	1.0000	1.0000	0.2889	0.3249
5	240	0.4446	0.2717	0	1.0000	1.0000	0.4100	0.4791
20	60	0.5161	0.2011	0.1141	0.8221	0.7080	0.4642	0.5680
					ity: Wet site			
1	600	0.3260	0.3121	0	1.0000	1.0000	0.3008	0.3508
5	120	0.4516	0.2686	0	1.0000	1.0000	0.4026	0.4997
20	30	0.5508	0.1801	0.1914	0.8138	0.6223	0.4835	0.6180
	600	0.0000	Simpse	on's diversi	ity: Dry site	1 0000	0.000	
1	600				1.0000			
5	120	0.4380	0.2757	0	1.0000	1.0000	0.3882	0.4879
20	30	0.4815	0.2175	0.1141	0.8221	0.7080	0.4002	0.5627
	400	0.0050			ty: SAND		0.0505	0.010.
-	400	0.2859	0.2750	0	1.0000	1.0000	0.2585	0.3125
5	80	0.3768	0.2565	0 1005	1.0000	1.0000	0.3197	0.4338
20	20	0.4248	0.1779	0.1895	0.7700	0.5805	0.3415	0.5080
	200	1 0 2004			ty: SAND		0.2700 T	0.0150
1	200	0.3084	0.2753	0	1.0000	1.0000	0.2700	0.3468
5	40	0.3784	0.2685		1.0000	1.0000	0.2926	0.4643
20	10	0.4860	0.1833	0.1969	0.7700	0.5732	0.3548	0.6171
1	200	0.2620		on's aiversi	ty: SAND I		0.2245	0.200=
	200	0.2629	0.2735	U	1.0000	1.0000	0.2245	0.3007
5	40	0.3751	0.2473	0	1.0000	1.0000	0.2960	0.4541

Table 7.1 (continued).

Grain (m²)	n	Mean	sd	min	max	Range	Lower 95% CI	Upper 95% CI
			Numbe	er of specie	s: STEPP	E All sites	1	
1	400	0.2987	0.3189	0	1.0000	1.0000	0.2673	0.3300
5	80	0.4451	0.2636	0	1.0000	1.0000	0.3864	0.5037
20	20	0.5655	0.1605	0.2257	0.8221	0.5964	0.4905	0.6406
		- 150 P.A.	Simpse	on's diversi	ty: STEPP	E Wet sites	S	
1	200	0.2958	0.2962	0	1.0000	1.0000	0.2544	0.3371
5	40	0.4458	0.2495	0	1.0000	1.0000	0.3660	0.5256
20	10	0.5569	0.1237	0.3740	0.7821	0.4081	0.4685	0.6454
			Simpse	on's diversi	ty: STEPP	E Dry sites		
1	200	0.3016	0.3407	0	1.0000	1.0000	0.2541	0.3491
5	40	0.4443	0.2802	0	1.0000	1.0000	0.3547	0.5339
20	10	0.5740	0.1973	0.2257	0.8221	0.5964	0.4328	0.7151
			Simpse	on's diversi	ty: GARIO	SUE All site	es	
1	400	0.3366	0.3539	0	1.0000	1.0000	0.3018	0.3714
5	80	0.5120	0.2805	0	1.0000	1.0000	0.4495	0.5744
20	20	0.5581	0.2344	0.1141	0.8138	0.6996	0.4484	0.6678
			Simpse	on's diversi	ty: GARIO	UE Wet si	tes	1.0449
1	200	0.3733	0.3553	0	1.0000	1.0000	0.3237	0.4228
5	40	0.5292	0.2721	0	0.8676	0.8676	0.4422	0.6162
20	10	0.6093	0.2171	0.1914	0.8158	0.6223	0.4540	0.7646
	100		Simps	on's divers	ity: GARIC	GUE Dry sit	tes	
1	200	0.2999	0.3494	0	1.0000	1.0000	0.2512	0.3487
5	40	0.4947	0.2912	0	1.0000	1.0000	0.4016	0.5879
20	10	0.5069	0.2510	0.1141	0.7978	0.6837	0.3273	0.6865

Figure 7.1. Number of species, species abundances, Shannon (log₂) and Simpson's diversity at the sites (see Table 6.1 for details of sites). Mean (bold line), and lower and upper 95% confidence intervals of the mean (fine lines) for the data are shown.

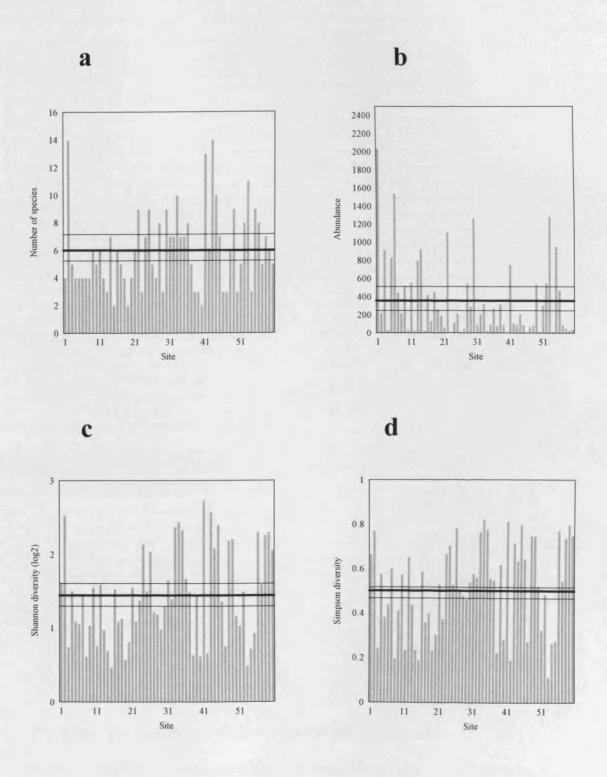


Table 7.2. Spearman's rank correlations of the number of species and heterogeneity used for testing hypothesis H_1 : The higher the heterogeneity the more species that are present. Results are for (1) combined data from sand, steppe and garigue habitats, from wet and dry periods combined, and wet and dry periods separately, and (2) for each habitat using combined data from wet and dry periods, and wet and dry periods separately. Significance is 2-tailed for all cases, and significance levels are indicated as: ns (not significant), * (0.05), ** (0.01), *** (<0.001). See Table 6.5 for full list of environmental variables and Table 6.1 for list of sites with habitat types and periods.

Sites: Habitat type/Period	Number of quadrats	Spearman's rank correlation	P	Significance level
All sites	1200	0.133	< 0.001	***
All wet sites	600	0.123	0.002	**
All dry sites	600	0.141	0.001	**
SAND: all sites	400	0.087	0.083	ns
SAND: all wet sites	200	0.317	< 0.001	***
SAND: all dry sites	200	-0.072	0.313	ns
STEPPE: all sites	400	0.230	< 0.001	***
STEPPE: all wet sites	200	0.206	0.003	**
STEPPE: all dry sites	200	0.257	< 0.001	***
GARIGUE: all sites	400	0.206	< 0.001	***
GARIGUE: all wet sites	200	0.186	0.008	**
GARIGUE: all dry sites	200	0.219	0.002	**

Table 7.3. Spearman's rank correlations of the abundances of species (\log_{x+1} transformed) and heterogeneity used for testing hypothesis H_2 : The higher the heterogeneity, the higher the abundances of species. Results are for (1) combined data from sand, steppe and garigue habitats, from wet and dry periods combined, and wet and dry periods separately, and (2) for each habitat using combined data from wet and dry periods, and wet and dry periods separately. Significance is 2-tailed for all cases, and significance levels are indicated as: ns (not significant), * (0.05), ** (0.01), *** (<0.001). See Table 6.5 for full list of environmental variables and Table 6.1 for list of sites with habitat types and periods.

Sites: Habitat type/Period	Number of quadrats	Spearman's rank correlation	P	Significance level
All sites	1200	-0.006	0.849	ns
All wet sites	600	-0.030	0.459	ns
All dry sites	600	0.030	0.459	ns
SAND: all sites	400	0.112	0.026	*
SAND: all wet sites	200	0.347	< 0.001	***
SAND: all dry sites	200	-0.046	0.515	ns
STEPPE: all sites	400	0.250	< 0.001	***
STEPPE: all wet sites	200	0.258	< 0.001	***
STEPPE: all dry sites	200	0.299	< 0.001	***
GARIGUE: all sites	400	0.083	0.096	ns
GARIGUE: all wet sites	200	0.122	0.085	ns
GARIGUE: all dry sites	200	0.078	0.273	ns

H_3 : The higher the complexity the more species that are present

There was a significant positive correlation between complexity and number of species for most habitat types and period combinations (Table 7.4) indicating

that increased complexity is associated with a higher number of species. The association was not significant for neither dry sand sites nor dry steppe sites.

Table 7.4. Spearman's rank correlations of the number of species and complexity used for testing hypothesis H_3 : The higher the complexity the more species that are present. Results are for (1) combined data from sand, steppe and garigue habitats, from wet and dry periods combined, and wet and dry periods separately, and (2) for each habitat using combined data from wet and dry periods, and wet and dry periods separately. Significance is 2-tailed for all cases, and significance levels are indicated as: ns (not significant), * (0.05), ** (0.01), *** (<0.001). See Table 6.5 for full list of environmental variables and Table 6.1 for list of sites with habitat types and periods.

Sites: Habitat type/Period	Number of quadrats	Spearman's rank correlation	P	Significance level
All sites	1200	0.141	< 0.001	***
All wet sites	600	0.180	< 0.001	***
All dry sites	600	0.086	0.035	**
SAND: all sites	400	0.177	< 0.001	***
SAND: all wet sites	200	0.199	0.005	**
SAND: all dry sites	200	0.090	0.204	ns
STEPPE: all sites	400	0.143	0.004	**
STEPPE: all wet sites	200	0.354	< 0.001	***
STEPPE: all dry sites	200	-0.074	0.299	ns
GARIGUE: all sites	400	0.223	< 0.001	***
GARIGUE: all wet sites	200	0.184	0.009	**
GARIGUE: all dry sites	200	0.268	< 0.001	***

H₄: The higher the complexity the higher the abundances of species

Correlations between complexity and the abundances of species were not significant for steppe (dry sites), garigue (wet sites), nor when data were pooled from all sites (Table 7.5). This indicates that increased complexity is not associated with higher abundances of species. The correlations were positive for sand (all sites, wet sites, dry sites), steppe (all sites, wet sites) and garigue (all sites, dry sites).

Table 7.5. Spearman's rank correlations of the abundances of species (\log_{x+1} transformed) and complexity used for testing hypothesis H_d : The higher the complexity the higher the abundances of species. Results are for (1) combined data from sand, steppe and garigue habitats, from wet and dry periods combined, and wet and dry periods separately, and (2) for each habitat using combined data from wet and dry periods, and wet and dry periods separately. Significance is 2-tailed for all cases, and significance levels are indicated as: ns (not significant), * (0.05), ** (0.01), *** (<0.001). See Table 6.5 for full list of environmental variables and Table 6.1 for list of sites with habitat types and periods.

Sites: Habitat type/Period	Number of quadrats	Spearman's rank correlation	P	Significance level	
All sites	1200	0.044	0.126	ns	
All wet sites	600	0.064	0.119	ns	
All dry sites	600	0.035	0.394	ns	
SAND: all sites	400	0.235	< 0.001	***	
SAND: all wet sites	200	0.258	< 0.001	***	
SAND: all dry sites	200	0.142	0.045	*	
STEPPE: all sites	400	0.261	< 0.001	***	
STEPPE: all wet sites	200	0.446	< 0.001	***	
STEPPE: all dry sites	200	0.003	0.964	ns	
GARIGUE: all sites	400	0.152	0.002	**	
GARIGUE: all wet sites	200	0.122	0.086	ns	
GARIGUE: all dry sites	200	0.205	0.004	**	

The results of correlations for Hypotheses H_l to H_d for some of the habitat type/period combinations were not significant when data were pooled (e.g. all wet and all dry sites for sand), yet positive correlations were achieved when these were correlated by period separately (e.g. all wet sand sites, see Tables 7.2 to 7.5). Combining the data from the two periods can result in associations from the individual periods being lost. This is because Spearman's rank correlation ranks the data, for each of the variables (i.e. heterogeneity or complexity, and number of species or abundances of species) before correlations are carried out (Kirkwood, 1998; Dytham, 2003). To obtain general trends from the data it is useful to consider pooled data; but to determine specific associations from the habitat types at the two periods, using data from these is more informative (Table 7.6).

Table 7.6. Summary of results for Hypotheses H_1 to H_4 for wet and dry periods at the habitat types (see Table 6.7 for descriptions of hypotheses, and results of Spearman's rank correlations for all habitat type/period combinations). $\sqrt{-}$ accept hypothesis; X= reject hypothesis.

Sites: Habitat type/Period	H_1	H_2	H_3	H_4
SAND: all wet sites	√	V	V	V
SAND: all dry sites	X	X	X	V
STEPPE: all wet sites	V	V	V	V
STEPPE: all dry sites	V	V	X	X
GARIGUE: all wet sites	1	X	V	X
GARIGUE: all dry sites	V	X	V	V

 H_5 : Some types of heterogeneity affect number of species independently of total complexity

 H_6 : Some types of heterogeneity affect abundances of species independently of total complexity

Results for the environmental variables are in Appendix 11 and results of partial correlations for testing Hypotheses H_5 and H_6 are in Appendix 12. There are significant correlations (positive and negative) between number of species and components of habitat structure (i.e. principal structures, see Section 7.2.3.2), and between species abundances and principal structures. Showing these correlations in a grid (Table 7.7) simplifies interpretation; listing significant principal structures for each habitat type reduces the data further and provides the easiest interpretation of these data (Table 7.8). Some types of habitat structure (heterogeneity) affect number of species and abundances independently of total complexity.

Table 7.7. Summary of the partial correlation results between number of species and components of habitat structure, and species abundances and components of habitat structure. (See Appendix 12 for more details). Only significant correlations are shown; negative (-) or positive (+). Empty boxes in grid denote no significance.

		Num	ber of s	species	and co	ompon	ents of	habite	at struc	cture		
	All sites	All wet sites	All dry sites	Sand: all sites	Sand: all wet sites	Sand: all dry sites	Steppe: all sites	Steppe: all wet sites	Steppe: all dry sites	Garigue: all sites	Garigue: all wet sites	Garigue: all dry sites
Soil			-	-	-		•		•			
Leaf litter	+	+		+	+		+	+			+	
Shingle		-		_	-	-	+		+			
Stone	-						+		+			
Rock			+	+	+		+	+	+	-	-	
Rubble	+	+	+				+	+	+	+	+	
Logs												+
Other wood	+	+										
Refuse	+		+				+			+	+	
Bryophyte	+	+										
Lichen		_						-		-		
Green grass (0-10)				+	+	+	-					
Green grass (10-110)	+	+	+	+	+	+	-	+	_	+		
Dry grass (0-10)		+	-	+	+		-		-	+		
Dry grass (10-110)	+	+	+		+	-		-	_	+	+	+
Annual (0-10)		+			+							
Annual (10-110)	+		+			_			:			
Herbaceous (0-10)		+					+		+			
Herbaceous (10-110)		+	-	+			+		+		-	-
Herbaceous (>110)	-		-							-		-
Shrub (0-10)	-	-						-			-	
Shrub (10-110)	-	-	_				-	-		-	-	-
Shrub (>110)	-	-	-				-	-		-		-
Tree (>110)		-		-	-							

Table 7.7 (continued).

Species	ahundances	and component	s of habita	t structure
Species	uvunuunces	unu componem	s vi nuvuui	SHUCLUTE

		Specie	S avan			<u> </u>		,	ui sii u			
	All sites	All wet sites	All dry sites	Sand: all sites	Sand: all wet sites	Sand: all dry sites	Steppe: all sites	Steppe: all wet sites	Steppe: all dry sites	Garigue: all sites	Garigue: all wet sites	Garigue: all dry sites
Soil	+	+					ı					
Leaf litter		+		1			+	+				
Shingle	-	-	-	-	-	-		-	+			-
Stone	-	_	-	-		_			+			-
Rock	-	_				-	+		+	_		-
Rubble	+	+					+	+	+	+	+	
Logs												+
Other wood												
Refuse			+						+	+	+	+
Bryophyte	-	-	-				+	+		-	-	
Lichen		_						-			-	
Green grass (0-10)		-	+	+		+					-	+
Green grass (10-110)	+	+	+	+	+	+	+	+		+		+
Dry grass (0-10)	·	+			+		-		-	+		+
Dry grass (10-110)		+	-		+	-	-	-	-	+	+	+
Annual (0-10)					+				-	-	-	
Annual (10-110)	+	+	+	+		+		+	+	+	+	+
Herbaceous (0-10)		+	-	+			+	+	+		+	-
Herbaceous (10-110)		+	-	+	+		-	-	+		+	-
Herbaceous (>110)			-				-	-				
Shrub (0-10)	-	-	ļ				_	-			-	-
Shrub (10-110)	-	-	-				-	-		-	-	-
Shrub (>110)	-		-				-	-		-		-
Tree (>110)	-	-			-		-					

Table 7.8. Reduced data (see Section 7.1.2) for partial correlations showing principal structures that have significant negative and positive correlations for number of species and abundances at the three habitat types (data used in each case are for all sites combined for each habitat type). See Appendix 12 for further details.

Positive	Positive	Positive
Number of species	Number of species	Number of species
Leaf litter	Leaf litter	Rubble
Rock	Shingle	Refuse
Green grass	Stone	Green grass
Dry grass	Rock	Dry grass
Herbaceous	Rubble	
	Refuse	
	Herbaceous	
Abundances	Abundances	Abundances
Green grass	Leaf litter	Rubble
Annual	Rock	Refuse
Herbaceous	Rubble	Green grass
Tieredecous	Bryophyte	Dry grass
	Green grass	Annual
	Herbaceous	1 Innau
Positive	Positive	Positive
1 ositive	Tositive	1 USITIVE
SAND	STEPPE	GARIGUE
Negative	Negative	Negative
Number of species	Number of species	Number of species
Soil	Soil	Rock
Shingle	Green grass	Lichen
8		
	Dry grass	Herbaceous
Tree	Dry grass Shrub	Herbaceous Shrub
	Dry grass Shrub	Herbaceous Shrub
	Shrub	
Tree <u>Abundances</u>	Shrub <u>Abundances</u>	Shrub <u>Abundances</u>
Tree	Shrub	Shrub
Tree Abundances Shingle Stone	Shrub <u>Abundances</u>	Shrub <u>Abundances</u>
Tree <u>Abundances</u> Shingle	Shrub <u>Abundances</u> Soil	Shrub <u>Abundances</u> Rock
Tree Abundances Shingle Stone	Shrub Abundances Soil Dry grass	Shrub Abundances Rock Bryophyte
Tree Abundances Shingle Stone	Shrub Abundances Soil Dry grass Herbaceous	Shrub Abundances Rock Bryophyte Annual
Tree Abundances Shingle Stone	Shrub Abundances Soil Dry grass Herbaceous Shrub	Shrub Abundances Rock Bryophyte Annual

Some principal structures are positively associated with number of species and abundances in some habitats, and negatively so in others (e.g. rock, dry grass). In some cases a principal structure may be positively associated in a habitat in the wet period, and negatively so in the dry period (e.g. green grass at steppe sites).

 H_7 : The number of species increases as spatial scale increases H_8 : The abundances of species increases as spatial scale increases

There is an increase in all habitat types in the number of species, abundance and diversity as the spatial scale increases (Table 7.1 and Figure 7.2). This increase also exists when sites are considered together (all sites), or separately as wet or dry period sites (Figure 7.3).

Figure 7.2. Number of species, species abundances, Shannon (\log_2) diversity and Simpson's diversity at the three levels of grain. These are indicated on the x axis in each case ($1=1\,\text{m}^2$, $5=5\,\text{m}^2$, $20=20\,\text{m}^2$). For each level of grain there are three sets of plotted data: in each case the left hand bar are data for sand, the central bar for steppe, and the right hand bar for garigue. In each figure the mean (marker) and lower and upper 95% confidence intervals of the mean (crosslines) for the data are shown.

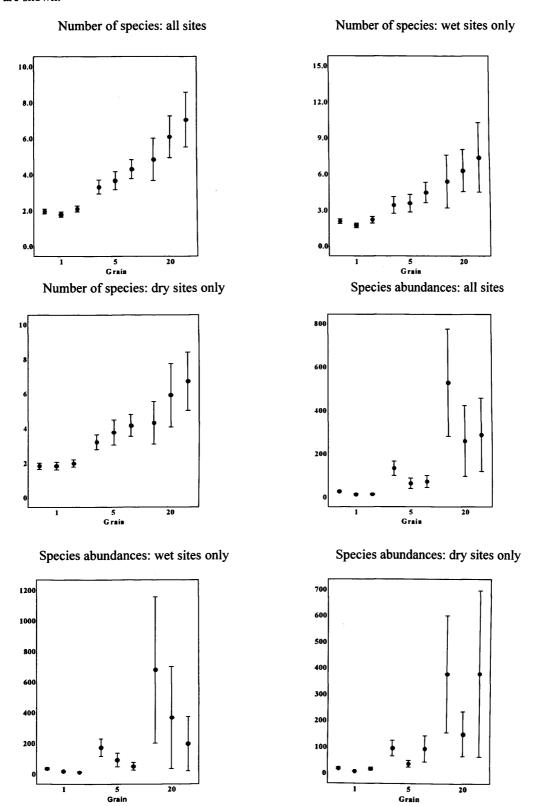
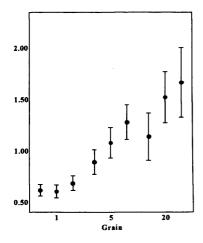
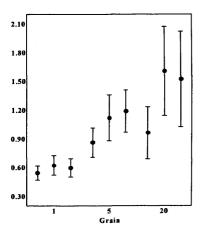


Figure 7.2 (continued).

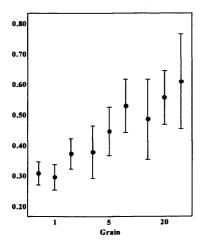
Shannon diversity: all sites



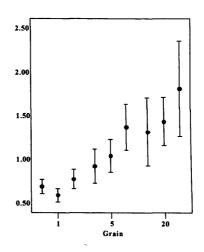
Shannon diversity: dry sites only



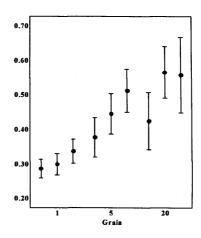
Simpson's diversity: wet sites only



Shannon diversity: wet sites only



Simpson's diversity: all sites



Simpson's diversity: dry sites only

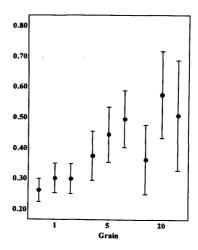
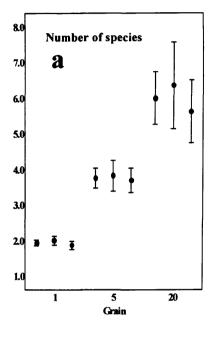
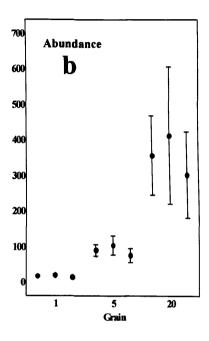
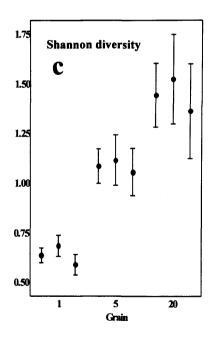
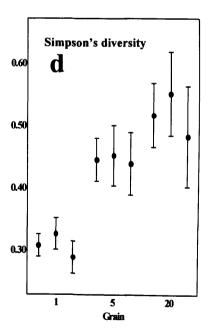


Figure 7.3. Number of species (a), species abundances (b), Shannon (log₂) diversity (c) and Simpson's diversity (d) for the site/period combinations at the three levels of grain (1=1m², 5=5 m², 20=20 m²). The site/period combinations for each grain level are: left-hand bar=all sites, central bar=wet sites only, right-hand bar=dry sites only. Mean (marker) and lower and upper 95% confidence intervals of the mean (crosslines) for the data are shown.



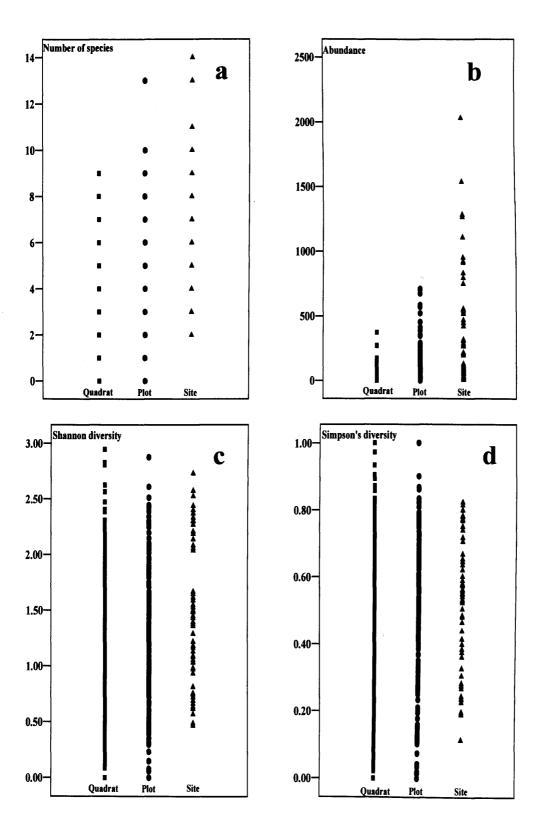






Plotting the data for number of species, abundances and diversity for each quadrat, plot and site (rather than mean and 95% CI as is the case in Figure 7.2 for site/periods) shows that number of species and abundances are scale dependent; both increasing as scale increases (this being more marked for abundances, Figure 7.4). The data for both Shannon and Simpson's diversity indicate that values for these indices are similar across scales (Figure 7.4). Thus, although mean and 95% CI data clearly show scale dependence in diversity (Figure 7.3 and Table 7.1), individual quadrats and plots may have values for these that are greater than those for sites (Table 7.1).

Figure 7.4. Number of species (a), species abundances (b), Shannon (\log_2) (c), and Simpson's diversity (d) for the three grain levels. Data show individual values for quadrats (1m^2 , n=1200), plots (5m^2 , n=240), and sites (20m^2 , n=60).



The results of ANOVA (with *post hoc* tests, Table 7.9) support the results of the descriptive statistics, indicating significant differences between all three levels of grain for number of species and abundances of species (as well as Shannon and Simpson's diversity).

Table 7.9. Results of ANOVA to assess if the number of species, abundances, Shannon (log₂) and Simpson's diversities from the three levels of grain (1m², 5m² and 20m²) differ significantly. By convention lines are drawn under combinations that do not differ significantly (here all combinations differ significantly and there are no underlined combinations).

Number of Sp	ecies	A 1 . CV.	. (4210)142		
	10		iance (ANOVA)	P.	T 0: 10
Source	df	Sum of sqs	Mean sqs	F ratio	Significance
Between gps	2	3.71	1.85	35.69	< 0.001
Within gps	1497	77.77	0.05		
Total	1499	81.48			
	Post hoc test usi		significant diffe)
Grain level	Grain level	Mean	Lower 95%	Upper 95	Mark the Au
(I)	(J)	difference	Confidence	Confidence	Significance
		(I-J)	Interval	Interval	
1m ²	5m ²	-0.11	-0.14	-0.08	< 0.001
	20m ²	-0.17	-0.23	-0.11	< 0.001
5m ²	1 m ²	0.11	0.08	0.14	< 0.001
	20m ²	-0.06	-0.12	0.01	0.05
20m ²	1 m ²	0.17	0.11	0.23	< 0.001
	5m ²	0.06	-0.01	0.12	0.05
	of the state of the		$\frac{\text{sults}}{20\text{m}^2} = \frac{5\text{m}^2}{2}$		
Abundance	16	Analysis of Var Sum of sqs	iance (ANOVA)		
Source	df	Sum of sas			GC
Between gps			Mean sqs	F ratio	
Within gps	2	949.28	474.64	211.82	Significance
	1497	949.28 3354.41			
	1497 1499	949.28 3354.41 4303.68	474.64 2.24	211.82	<0.001
	1497 1499	949.28 3354.41 4303.68 ng Fisher's least	474.64 2.24 significant diffe	211.82 rence test (LSD)	<0.001
Total	1497 1499 Post hoc test usi	949.28 3354.41 4303.68 ng Fisher's least Mean	474.64 2.24 significant diffe Lower 95%	211.82 rence test (LSD) Upper 95	<0.001
Total Grain level	1497 1499 Post hoc test usi Grain level	949.28 3354.41 4303.68 ng Fisher's least Mean difference	474.64 2.24 significant diffe Lower 95% Confidence	211.82 rence test (LSD) Upper 95 Confidence	<0.001
Total Grain level (I)	1497 1499 Post hoc test usi Grain level (J)	949.28 3354.41 4303.68 ng Fisher's least Mean difference (I-J)	significant diffe Lower 95% Confidence Interval	211.82 rence test (LSD) Upper 95 Confidence Interval	<0.001 Significance
Total Grain level	1497 1499 Post hoc test usi Grain level (J) 5m ²	949.28 3354.41 4303.68 ng Fisher's least Mean difference (I-J) -1.53	significant diffe Lower 95% Confidence Interval -1.73	211.82 rence test (LSD) Upper 95 Confidence Interval -1.32	<0.001 Significance
Total Grain level (I) 1m ²	1497 1499 Post hoc test usi Grain level (J) 5m ² 20m ²	949.28 3354.41 4303.68 ng Fisher's least Mean difference (I-J) -1.53 -3.15	significant diffe Lower 95% Confidence Interval -1.73 -3.54	211.82 rence test (LSD) Upper 95 Confidence Interval -1.32 -2.76	<0.001 Significance <0.001 <0.001
Total Grain level (I)	1497 1499 Post hoc test usi Grain level (J) 5m² 20m² 1m²	949.28 3354.41 4303.68 ng Fisher's least Mean difference (1-J) -1.53 -3.15 1.53	significant diffe Lower 95% Confidence Interval -1.73 -3.54 1.32	211.82 rence test (LSD) Upper 95 Confidence Interval -1.32 -2.76 1.73	<0.001 Significance <0.001 <0.001 <0.001
Grain level (I) 1m ² 5m ²	1497 1499 Post hoc test usi Grain level (J) 5m² 20m² 1m² 20m²	949.28 3354.41 4303.68 ng Fisher's least Mean difference (I-J) -1.53 -3.15 1.53 -1.63	474.64 2.24 significant diffe Lower 95% Confidence Interval -1.73 -3.54 1.32 -2.05	211.82 rence test (LSD) Upper 95 Confidence Interval -1.32 -2.76 1.73 -1.20	<0.001 Significance <0.001 <0.001 <0.001 <0.001
Total Grain level (I) 1m ²	1497 1499 Post hoc test usi Grain level (J) 5m² 20m² 1m² 20m² 1m²	949.28 3354.41 4303.68 ng Fisher's least Mean difference (I-J) -1.53 -3.15 1.53 -1.63 3.15	474.64 2.24 significant diffe Lower 95% Confidence Interval -1.73 -3.54 1.32 -2.05 2.76	211.82 rence test (LSD) Upper 95 Confidence Interval -1.32 -2.76 1.73 -1.20 3.54	<0.001 Significance <0.001 <0.001 <0.001
Grain level (I) 1m ² 5m ²	1497 1499 Post hoc test usi Grain level (J) 5m² 20m² 1m² 20m²	949.28 3354.41 4303.68 ng Fisher's least Mean difference (I-J) -1.53 -3.15 1.53 -1.63 3.15 1.63	474.64 2.24 significant diffe Lower 95% Confidence Interval -1.73 -3.54 1.32 -2.05 2.76 1.20	211.82 rence test (LSD) Upper 95 Confidence Interval -1.32 -2.76 1.73 -1.20	<0.001 Significance <0.001 <0.001 <0.001 <0.001
Grain level (I) 1m ² 5m ²	1497 1499 Post hoc test usi Grain level (J) 5m² 20m² 1m² 20m² 1m² 5m²	949.28 3354.41 4303.68 ng Fisher's least Mean difference (I-J) -1.53 -3.15 1.53 -1.63 3.15 1.63	474.64 2.24 significant diffe Lower 95% Confidence Interval -1.73 -3.54 1.32 -2.05 2.76 1.20 sults	211.82 rence test (LSD) Upper 95 Confidence Interval -1.32 -2.76 1.73 -1.20 3.54 2.04	<0.001 Significance <0.001 <0.001 <0.001 <0.001 <0.001 <0.001

Table 7.9 (continued).

Shannon diver	rsity				·
	and the second second	Analysis of Var	riance (ANOVA)		
Source	df	Sum of sqs	Mean sqs	F ratio	Significance
Between gps	2	22.99	11.50	77.89	< 0.001
Within gps	1497	220.98	0.15		
Total	1499	243.97			
	Post hoc test us	ing Fisher's least	t significant diffe	rence test (LSD)	
Grain level (I)	Grain level (J)	Mean difference (I-J)	Lower 95% Confidence Interval	Upper 95 Confidence Interval	Significance
1m ²	5m ²	-0.26	-0.31	-0.21	< 0.001
	20m ²	-0.45	-0.55	-0.35	< 0.001
$5m^2$	1 m ²	0.26	0.21	0.31	< 0.001
	20m ²	-0.19	-0.29	-0.08	< 0.001
20m ²	l m ²	0.45	0.35	0.55	< 0.001
	5m ²	0.19	0.08	0.29	0.001
Simpson's dive	ersity	A 1 ' CV	· (ANOVA)		
0	10		riance (ANOVA)		0: :0
Source	df	Sum of sqs	Mean sqs	F ratio	Significance
Between gps	2	3.71	1.85	35.69	0 001
Within gps	1497		0.0#		< 0.001
Lotal		77.77	0.05		<0.001
I Otal	1499	81.48			<0.001
Total	1499	81.48 ing Fisher's leas	t significant diffe		<0.001
Grain level (I)	Post hoc test us Grain level (J)	81.48		rence test (LSD) Upper 95 Confidence Interval	
Grain level	Post hoc test us Grain level (J) 5m²	81.48 ing Fisher's leas Mean difference	t significant diffe Lower 95% Confidence	Upper 95 Confidence	
Grain level (I)	Post hoc test us Grain level (J) 5m² 20m²	81.48 ing Fisher's leas Mean difference (I-J)	t significant diffe Lower 95% Confidence Interval	Upper 95 Confidence Interval	Significance
Grain level (I)	1499 Post hoc test us Grain level (J) 5m² 20m² 1m²	81.48 ing Fisher's leas Mean difference (I-J) -0.11 -0.17	t significant diffe Lower 95% Confidence Interval -0.14 -0.23 0.08	Upper 95 Confidence Interval	Significance
Grain level (I)	1499 Post hoc test us Grain level (J) 5m² 20m² 1m² 20m²	81.48 ing Fisher's leas Mean difference (I-J) -0.11	t significant diffe Lower 95% Confidence Interval -0.14 -0.23	Upper 95 Confidence Interval -0.08	Significance <0.001 <0.001
Grain level (I)	1499 Post hoc test us Grain level (J) 5m² 20m² 1m²	81.48 ing Fisher's leas Mean difference (I-J) -0.11 -0.17	t significant diffe Lower 95% Confidence Interval -0.14 -0.23 0.08	Upper 95 Confidence Interval -0.08 -0.11	<pre>Significance <0.001 <0.001 <0.001</pre>
Grain level (I) 1m ² 5m ²	1499 Post hoc test us Grain level (J) 5m² 20m² 1m² 20m²	81.48 ing Fisher's leas Mean difference (I-J) -0.11 -0.17 0.11	t significant diffe Lower 95% Confidence Interval -0.14 -0.23 0.08 -0.12	Upper 95 Confidence Interval -0.08 -0.11 0.14 0.01	<pre>Significance <0.001 <0.001 <0.001 <0.001 <0.005</pre>
Grain level (I) 1m² 5m²	1499 Post hoc test us Grain level (J) 5m² 20m² 1m² 20m² 1m² 5m²	81.48 ing Fisher's leas Mean difference (I-J) -0.11 -0.17 0.11 -0.06 0.17 0.06	t significant diffe Lower 95% Confidence Interval -0.14 -0.23 0.08 -0.12 0.11	Upper 95 Confidence Interval -0.08 -0.11 0.14 0.01 0.23 0.12	Significance <0.001 <0.001 <0.001 0.05 <0.001

Results for Spearman's rank correlations (using pooled data from the sites) between heterogeneity and number and abundances of species, and diversity (Table 7.10) show a positive correlation at the 1m² level of grain between heterogeneity and number of species, Shannon and Simpson's diversity, but not

Table 7.10. Spearman's rank correlations to assess relationships between number of species and species abundances with total heterogeneity and total complexity at the three levels of grain $(1m^2, 5m^2 \text{ and } 20m^2)$. All P are 2-tailed.

Total heterogeneity with Number of species

Grain (m²)	1	1	1	5	5	5	20	20	20
sites	n	r _s	P	n	rs	P	n	rs	P
all	1200	0.133	< 0.001	240	-0.014	0.824	60	-0.050	0.703
wet	600	0.123	0.002	120	0.022	0.808	30	0.106	0.576
dry	600	0.141	0.001	120	-0.124	0.055	30	-0.050	0.703

Total heterogeneity with Species abundances

Grain (m²)	1	1	1	5	5	5	20	20	20
sites	n	rs	P	n	r_s	P	n	rs	P
all	1200	-0.006	0.849	240	0.045	0.488	60	0.055	0.674
wet	600	-0.030	0.459	120	0.002	0.979	30	0.002	0.990
dry	600	0.030	0.459	120	-0.079	0.221	30	0.055	0.674

Total heterogeneity with Shannon diversity

Grain (m²)	1	1	1	5	5	5	20	20	20
sites	n	rs	P	n	rs	P	n	r _s	P
all	1200	0.154	< 0.001	240	-0.058	0.368	60	-0.108	0.410
wet	600	0.159	< 0.001	120	0.077	0.403	30	0.107	0.575
dry	600	0.147	< 0.001	120	-0.104	0.107	30	-0.108	0.410

Total heterogeneity with Simpson's diversity

		101	ut netero,	School in	этри	11 5 411, 615	•••		
Grain (m²)	1	1	1	5	5	5	20	20	20
sites	n	r _s	P	n	rs	P	n	r _s	P
all	1200	0.175	< 0.001	240	-0.099	0.127	60	-0.176	0.177
wet	600	0.203	< 0.001	120	0.030	0.742	30	-0.071	0.711
dry	600	0.145	< 0.001	120	-0.079	0.224	30	-0.176	0.177

Total complexity with Number of species

Grain (m ²)	1	1	1	5	5	5	20	20	20		
sites	n	r _s	P	n	rs	P	n	rs	P		
all	1200	0.141	< 0.001	240	-0.014	0.827	60	-0.062	0.636		
wet	600	0.180	< 0.001	120	0.055	0.549	30	0.146	0.442		
dry	600	0.086	0.035	120	-0.155	0.016	30	-0.062	0.636		

Total complexity with Species abundances

Grain (m²)	1	1	1	5	5	5	20	20	20
sites	n	rs	P	n	rs	P	n	rs	P
all	1200	0.044	0.126	240	0.032	0.624	60	0.058	0.658
wet	600	0.064	0.119	120	-0.004	0.969	30	-0.005	0.980
dry	600	0.035	0.394	120	-0.119	0.065	30	0.058	0.658

Table 7.10 (continued).

Total complexity with Shannon diversity

Grain (m ²)	1	1	1	5	5	5	20	20	20
sites	n	rs	P	n	rs	P	n	rs	P
all	1200	0.146	< 0.001	240	-0.084	0.192	60	-0.156	0.234
wet	600	0.200	< 0.001	120	0.068	0.461	30	0.090	0.636
dry	600	0.077	0.059	120	-0.140	0.030	30	-0.156	0.234

Total complexity with Simpson's diversity

Grain (m²)	1	1	1	5	5	5	20	20	20
sites	n	r _s	P	n	T _S	P	n	rs	P
all	1200	0.166	< 0.001	240	-0.107	0.098	60	-0.227	0.081
wet	600	0.231	< 0.001	120	0.053	0.562	30	-0.088	0.644
dry	600	0.080	0.051	120	-0.091	0.159	30	-0.227	0.081

with abundances. Thus, number of species and diversity, but not abundances, are significantly positively correlated at the 1m² level of grain. There are no significant correlations at the 5m² nor 20m² levels of grain. The results are similar for complexity (Table 7.10), with positive correlations at the 1m² level of grain between complexity and number of species, Simpson's and Shannon diversity, but not with abundances. In general, positive correlations are present only at the 1m² level of grain (Table 7.10). At spatial scales higher than this, heterogeneity and complexity were not correlated with number of species nor diversity.

H_9 : There is more variation in heterogeneity in some habitat types than in others

 H_{10} : There is more variation in complexity in some habitat types than in others

Combining all sites (wet and dry), the habitat types order from lowest to highest for heterogeneity and complexity as: (1) sand, (2) steppe, (3) garigue (Table 7.11, Figure 7.5). Heterogeneity and complexity are greater in the wet period than the dry period at all habitat types (Figure 7.6).

Table 7.11. Mean, standard deviation (sd), minimum (min), maximum (max), range, lower and upper 95% confidence intervals of the mean (CI) for total heterogeneity and total complexity at all sites, wet sites combined and dry sites combined, and for each of the habitat types (all sites, wet sites and dry sites).

,			Total H	leterogene	rity		 	
Sites: Habitat type/Period	n	Mean	sd	Min	Max	Range	Lower 95% CI	Upper 95% CI
All sites	60	36.80	18.619	10	87	77	31.99	41.61
All wet sites	30	37.70	21.446	12	87	77	29.69	45.71
All dry sites	30	35.90	15.610	10	68	58	30.07	41.73
SAND: all sites	20	21.25	11.097	10	53	43	16.06	26.44
SAND: all wet sites	10	21.10	11.808	12	53	41	12.65	29.55
SAND: all dry sites	10	21.40	10.997	. 10	43	33	13.55	29.25
STEPPE: all sites	20	34.90	13.494	21	72	51	28.58	41.22
STEPPE: all wet sites	10	32.70	15.428	21	72	51	21.66	43.74
STEPPE: all dry sites	10	37.10	11.647	22	57	35	28.77	45.43
GARIGUE: all sites	20	54.25	13.871	33	87	54	47.76	60.74
GARIGUE: all wet sites	10	59.30	15.882	41	87	46	47.94	70.66
GARIGUE: all dry sites	10	49.20	9.864	33	68	35	42.14	56.26
			Total	Complexit	y			
Sites: Habitat type/Period	n	Mean	sd	Min	Max	Range	Lower 95% CI	Upper 95% CI
All sites	60	3799.50	1887.034	1203	8883	7680	3312.03	4286.97
All wet sites	30	4035.60	2200.852	1203	8883	7680	3213.79	4857.41
All dry sites	30	3563.40	1511.788	2073	7679	5606	2998.89	4129.91
SAND: all sites	20	2281.70	396.056	1203	3056	1853	2096.34	2467.06
SAND: all wet sites	10	2223.50	498.886	1203	3056	1853	1866.62	2580.38
SAND: all dry sites	10	2339.90	273.379	2073	2800	727	2144.34	2535.20
STEPPE: all sites	20	3074.65	788.113	2133	4606	2473	2705.80	3443.50
STEPPE: all wet sites	10	3107.70	905.156	2133	4606	2473	2460.19	3755.21
STEPPE: all dry sites	10	3041.60	699.659	2382	4416	2034	2541.09	3542.11
GARIGUE:	20	6042.15	1416.802	3121	8883	5762	5379.07	6705.23
all sites								
all sites GARIGUE: all wet sites	10	6775.60	1261.919	5427	8883	3456	5872.88	7678.32

Figure 7.5. Heterogeneity and complexity in the quadrats from all sites for the three habitat types (n=400 for each habitat type).

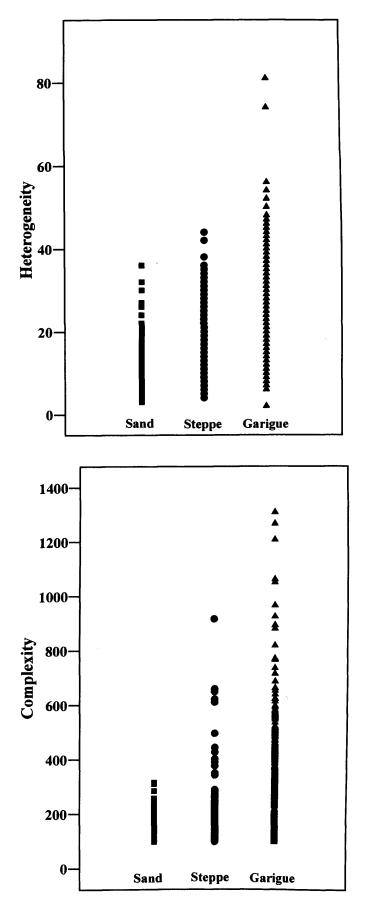
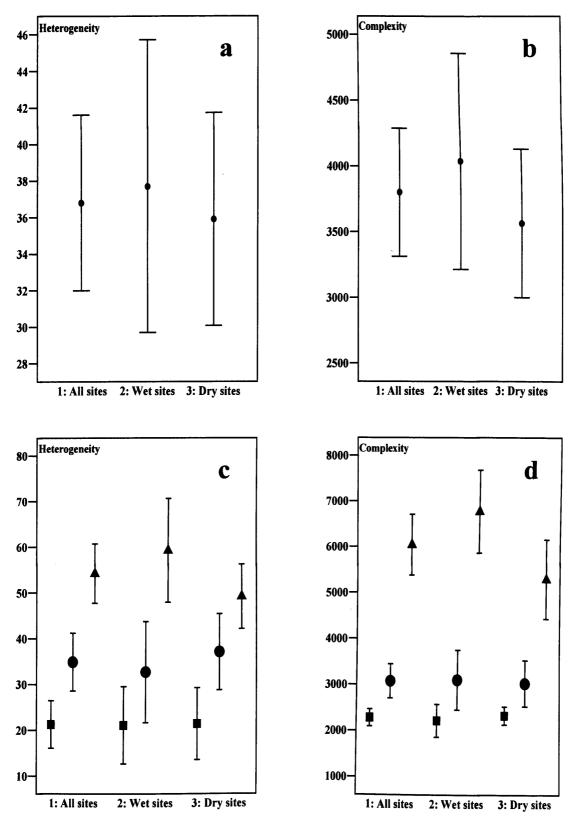


Figure 7.6. Heterogeneity and complexity for the habitat types and periods. (a) heterogeneity and (b) complexity for the three habitat types combined for all sites (n=60), wet sites (n=30) and dry sites (n=30). (c) heterogeneity and (d) complexity at sand (squares), steppe (circles) and garigue (triangles) habitat types for all sites (n=20) per type), wet sites (n=10) per type) and dry sites (n=10) per type). In each graph the mean (markers) and lower and upper 95% confidence intervals of the mean (crossbars) are shown.



Heterogeneity and complexity data for the sites (Table 7.1, Figures 7.5 and 7.6, Appendices 13 and 14) indicate that there is more variance in heterogeneity and complexity in some habitats than in others (Table 7.12). The means for the coefficient of variation for heterogeneity and complexity differ significantly (t=3.036, P=0.01) but there in no significant correlation between the variation for heterogeneity and complexity (Spearman's 0.070, P=0.829).

Table 7.12. Variation in heterogeneity and complexity at the habitat types and periods. There is no significant correlation between the variation for heterogeneity and complexity (Spearman's rank correlation=0.070, P=0.829). The means for the coefficient of variation for heterogeneity and complexity differ significantly (t=3.036, degrees of freedom 22, P=0.01; Levene's test for equality of variances: F=1.147, P=0.296).

	Coefficient of Varia	tion (%)
Habitat type/period	Heterogeneity	Complexity
All sites	50.6	27.8
All wet sites	56.9	54.5
All dry sites	43.5	42.4
Sand: all sites	52.2	17.4
Sand: wet sites	56.0	22.4
Sand: dry sites	51.4	11.7
Steppe: all sites	38.7	25.6
Steppe: wet sites	47.2	29.1
Steppe: dry sites	31.4	23.0
Garigue: all sites	25.6	23.4
Garigue: wet sites	26.8	18.6
Garigue: dry sites	20.0	22.7
Mean	41.69	26.55
Standard deviation	12.862	11.534
Lower 95% Confidence Interval	35.52	19.22
Upper 95% Confidence Interval	49.86	33.88

In general there is more variance in both heterogeneity and complexity in the wet period than in the dry period at all habitat types (Tables 7.13 and 7.14). Combining all sites (wet and dry), the habitat types order from lowest to highest for variance in heterogeneity as: (1) garigue, (2) steppe, (3) sand, and for variance in complexity as: (1) sand, (2) garigue, (3) steppe.

Table 7.13. The amount of variation in heterogeneity and complexity at the habitat types and periods. Variation is shown in descending order (where 1 indicates greatest variation).

1. Variatio	n in heterogene	eity and complex habitat types		order of variati	on at the
Habitat type	Period	Heterogeneity	Habitat type	Period	Complexity
	Wet	1		Wet	1
All	Wet and Dry	2	All	Dry	2
	Dry	3		Wet and Dry	3
	Wet	1		Wet	1
Sand	Wet and Dry	2	Sand	Wet and Dry	2
	Dry	3		Dry	3
	Wet	1		Wet	1
Steppe	Wet and Dry	2	Steppe	Wet and Dry	2
	Dry	3	1	Dry	3
	Wet	1		Wet and Dry	1
Garigue	Wet and Dry	2	Garigue	Dry	2
J	Dry	3		Wet	3
2. Variatio	n in heterogene	ity and complexi	ty: descending	order of variati	on for the
		periods by h			A developed to 2
Period	Habitat type	Heterogeneity	Period	Habitat type	Complexity
	Sand	1		Steppe	1
Wet and Dry	Steppe	2	Wet and Dry	Garigue	2
·	Garigue	3		Sand	3
	Sand	1		Steppe	1
Wet	Steppe	2	Wet	Sand	2
	Garigue	3		Garigue	3
	Sand	1		Steppe	1
Dry	Steppe	2	Dry	Garigue	2
•	Garigue	3	1	Sand	3

 H_{11} : Heterogeneity differs between the habitat types

 H_{12} : Complexity differs between the habitat types

H₁₃: Heterogeneity differs between the wet and dry periods at each habitat type

 H_{14} : Complexity differs between the wet and dry periods at each habitat type

 H_{15} : Heterogeneity differs between the wet and dry periods between the habitat types

 H_{16} : Complexity differs between the wet and dry periods between the habitat types

For habitats: There are significant differences in heterogeneity and complexity for all habitat types. Using all site combinations (Table 7.14) the habitat types order from lowest to highest for heterogeneity and complexity as: (1) sand, (2) steppe, (3) garigue.

For periods: There are significant differences in heterogeneity and complexity for many habitat type/period combinations. There were, however, no differences

for wet and dry periods at steppe (heterogeneity), and wet and dry periods at sand, and wet and dry periods at steppe (complexity) (Figure 7.6).

Table 7.14. ANOVA to assess if heterogeneity and complexity from the habitat types (sand, steppe, garigue) differ significantly for wet and dry sites, and to assess if heterogeneity and complexity from the habitat types combined (all sand, all steppe, all garigue) differ significantly. By convention lines are drawn under combinations that do not differ significantly. Quadrat data are used in all cases.

		Analysis of Var	iance (ANOVA)	CT :	113-1-5
Source	df	Sum of sqs	Mean sq	F ratio	Significance
Between gps	5	174.498	34.900	241.893	< 0.001
Within gps	1194	172.267	0.144		
Total	1199	346.765			
	Post hoc test usi	ng Fisher's least	significant diffe	rence test (LSD)	1-1-1-7-7-7-7
Unhitat tuma	Hobitat tumo	Mean	Lower 95%	Upper 95%	
Habitat type	Habitat type	difference	Confidence	Confidence	Significance
(I)	(J)	(I-J)	Interval Interval		
sand wet	sand dry	-0.19033	-0.2649	-0.1158	< 0.001
sand wet	steppe wet	-0.55213	-0.6267	-0.4776	< 0.001
sand wet	steppe dry	-0.58183	-0.6564	-0.5073	< 0.001
sand wet	garigue wet	-0.12231	-1.1968	-1.0478	< 0.001
sand wet	garigue dry	-0.88503	0.9595	-0.8105	< 0.001
sand dry	steppe wet	-0.36180	-0.4363	-0.2873	< 0.001
sand dry	steppe dry	-0.39150	-0.4660	-0.3170	< 0.001
sand dry	garigue wet	-0.93197	-1.0065	-0.8575	< 0.001
sand dry	garigue dry	-0.69469	-0.7692	-0.6202	< 0.001
steppe wet	steppe dry	-0.02970	-0.1042	0.0448	0.434
steppe wet	garigue wet	-0.57018	-0.6447	-0.4957	< 0.001
steppe wet	garigue dry	-0.33290	-0.4074	0.2584	< 0.001
steppe dry	garigue wet	-0.54048	-0.6150	-0.4660	< 0.001
steppe dry	garigue dry	-0.30320	-0.3777	0.2287	< 0.001
garigue wet	garigue dry	0.23728	0.1628	0.3118	< 0.001

sand wet sand dry sand wet steppe wet sand wet steppe dry sand wet garigue wet sand wet garigue dry sand dry steppe wet sand dry steppe dry sand dry garigue wet steppe wet garigue dry steppe wet garigue wet steppe wet garigue dry garigue wet garigue wet garigue wet garigue dry garigue wet garigue dry

Complexity- for	or sand, steppe, g	arigue: wet, dry			
	(6-2)		iance (ANOVA)		
Source	df	Sum of sqs	Mean sq	F ratio	Significance
Between gps	5	149.813	29.963	205.651	< 0.001
Within gps	1194	173.961	0.146	TELL	
Total	1199	323.773			
	Post hoc test usi	ng Fisher's least	significant diffe	rence test (LSD)	
Habitat tuma	Habitat truna	Mean	lean Lower 95% Upper		
Habitat type	Habitat type	difference	Confidence	Confidence	Significance
(1)	(J)	(I-J)	Interval	Interval	Significance Sign
sand wet	sand dry	-0.00258	-0.0775	0.0723	0.946
sand wet	steppe wet	-0.20410	-0.2790	-0.1292	< 0.001
sand wet	steppe dry	-0.18040	-0.2553	-0.1055	< 0.001
sand wet	garigue wet	-0.92399	-0.9989	-0.8491	< 0.001
sand wet	garigue dry	-0.70702	-0.7819	-0.6321	< 0.001

Table 7.14 (continued).

sand dry	steppe wet	-0.20152	-0.2764	-0.1266	< 0.001
sand dry	steppe dry	-0.17782	-0.2527	-0.1029	< 0.001
sand dry	garigue wet	-0.92141	-0.9963	-0.8465	< 0.001
sand dry	garigue dry	-0.70444	-0.7793	-0.6296	< 0.001
steppe wet	steppe dry	0.02370	-0.0512	0.0986	0.535
steppe wet	garigue wet	-0.71989	-0.7948	-0.6450	< 0.001
steppe wet	garigue dry	-0.50293	-0.5778	-0.4280	< 0.001
steppe dry	garigue wet	-0.74359	-0.8185	-0.6687	< 0.001
steppe dry	garigue dry	-0.52663	-0.6015	-0.4517	< 0.001
garigue wet	garigue dry	0.21696	0.1421	0.2919	< 0.001
		Res	ults		- 16.65

sand wet sand dry sand wet steppe wet sand wet steppe dry sand wet garigue wet sand wet garigue dry sand dry steppe wet sand dry steppe dry sand dry garigue wet steppe wet garigue dry steppe wet garigue wet steppe wet garigue wet steppe dry garigue dry garigue wet garigue dry

RESERVED SELECT		garigue wei	garigue dry		
Heterogeneity-	for all sand, all	steppe, all garis	que		
0			riance (ANOVA)		
Source	df	Sum of sqs	Mean sq	F ratio	Significance
Between gps	2	165.157	82.578	544.284	< 0.001
Within gps	1197	181.608	0.152	17. E 01 1	
Total	1199	346.765		THE PLE	1 1 7 2 1 1 1
	Post hoc test usi	ng Fisher's least	significant diffe	rence test (LSD)	
Habitat type (I)	Habitat type (J)	Mean difference (I-J)	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Significance
1	2	-0.47181	-0.5259	-0.4178	< 0.001
	3	-0.90850	-0.9625	-0.8545	< 0.001
2	3	-0.43669	-0.4907	-0.3826	< 0.001
-11, 11, 12	1 P 7 - 7 1	Res	sults		
	sand s	steppe sand ga	rigue steppe ga	arigue	(m) (m) (m)
	Silvery Service			The State of Parkers	
Complexity- fo	r all sand, all ste				
		Analysis of Var	iance (ANOVA)		11 11 11 11 11 11
Source	df	Sum of sqs	Mean sq	F ratio	Significance
Between gps	2	145.048	72.524	485.727	< 0.001
Within gps	1197	178.725	0.149		Mic in Care
Total	1199	323.773		17/13/11/20 T	
	Post hoc test using	ng Fisher's least	significant diffe	rence test (LSD)	
Habitat type (I)	Habitat type (J)	Mean difference (I-J)	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Significance
1	2	-0.19096	-0.2446	-0.1374	< 0.001
	3	-0.81422	-0.8678	-0.7606	< 0.001
2	3	-0.62326	-0.6769	-0.5697	< 0.001
		Res	ults		
	sand s	teppe sand ga	rigue steppe ga	rigue	

7.1.3. Habitat diversity

Heterogeneity and complexity are positively correlated at all grain levels (Table 7.15). Heterogeneity and complexity constitute two of the three axes of the McCoy and Bell (1991) 3-dimensional habitat structure model (the other is scale, Section 5.3) and their positive correlation suggests that habitat diversity indices (calculated using heterogeneity and complexity, Section 6.9.3) may be used to assess the effects of habitat structure on the number of species and species diversity. Further, the two habitat structure indices (Shannon and Simpson's) are positively correlated suggesting that either of them could be used for this purpose.

Table 7.15. Spearman's rank correlations (r_s) of number of species, abundances, species diversity and heterogeneity, complexity and habitat diversity (hd). For quadrats $(1m^2)$ n=1200, plots $(5m^2)$ n=240, sites $(20m^2)$ n=60. Significance is 2-tailed for all cases, and significance levels (sl) are indicated as: ns (not significant), * (0.05), ** (0.01), *** (0.01).

	Qua	uadrats Plots		ots	Sit	tes
Variables	r _s	sl	r _s	sl	r _s	sl
abundance with number of species	0.826	***	0.632	***	0.390	**
heterogeneity with number of species	0.133	***	-0.014	ns	-0.050	ns
heterogeneity with abundance	-0.006	ns	0.045	ns	0.055	ns
heterogeneity with Shannon (log ₂) diversity	0.154	***	-0.058	ns	-0.108	ns
heterogeneity with Simpson's diversity	0.175	***	-0.099	ns	-0.176	ns
complexity with heterogeneity	0.837	***	0.852	***	0.815	***
complexity with number of species	0.141	***	-0.014	ns	-0.062	ns
complexity with abundance	0.044	ns	0.032	ns	0.058	ns
complexity with Shannon (log ₂) diversity	0.146	***	-0.084	ns	-0.156	ns
complexity with Simpson's diversity	0.166	***	-0.107	ns	-0.227	ns
Shannon (log ₂) hd with number of species	0.113	***	0.221	**	0.312	*
Shannon (log ₂) hd with abundance	-0.022	ns	-0.082	ns	-0.172	ns
Shannon (log ₂) hd with Shannon (log ₂) diversity	0.134	***	0.308	***	0.311	*
Shannon (log ₂) hd with Simpson's diversity	0.162	***	0.328	***	0.266	*
Shannon (log ₂) hd with heterogeneity	0.923	***	0.934	***	0.920	***
Shannon (log ₂) hd with complexity	0.850	***	0.881	***	0.918	***
Simpson's hd with number of species	0.101	***	0.212	**	0.327	**
Simpson's hd with abundance	-0.027	ns	-0.096	ns	-0.192	ns
Simpson's hd with Shannon (log ₂) diversity	0.123	***	0.307	***	0.339	**
Simpson's hd with Simpson's diversity	0.151	***	0.332	***	0.297	**
Simpson's hd with heterogeneity	0.857	***	0.877	***	0.888	***
Simpson's hd with complexity	0.833	***	0.864	***	0.903	***
Shannon (log ₂) diversity with Simpson's diversity	0.960	***	0.922	***	0.950	***
Shannon (log ₂) hd with Simpson's hd	0.983	***	0.985	***	0.984	***

The data, however, show that the indices do not provide the same outcomes as do heterogeneity and complexity when these latter are considered separately (Table 7.16). When the habitat structure indices are assessed for efficacy using the criterion that they provide the same outcomes (for Spearman's rank correlations) as both heterogeneity and complexity (Table 7.16), the results show that the indices only do this for the 1m² grain level (quadrat). The habitat diversity indices provide positive correlations for all grain levels (quadrat, plot, and site). (Results for abundance are not significant for heterogeneity, complexity and both habitat diversity indices, for any of the grain levels, Table 7.16).

Table 7.16. An assessment of the efficacy of habitat diversity indices (Shannon (\log_2) and Simpson's) using the results of Spearman's rank correlations (r_s) of number of species, abundances, species diversity, heterogeneity, complexity and habitat diversity indices (Shannon (\log_2) and Simpson's). For quadrats (1m^2) n=1200, plots (5m^2) n=240, sites (20m^2) n=60 (see Table 6.2 for focus/grain classifications). Significance is indicated with $\sqrt{}$, and non-significance with X. All significant correlations are positive. See Table 7.15 for r_s values and significance levels. Efficacy is judged on the criterion that habitat diversity indices provide the same results as both heterogeneity and complexity for r_s (indicated as Yes and No).

		Heterogeneity	Complexity	Shannon habitat diversity	Simpson's habitat diversity	Efficacy?
	Grain					
Number	quadrat	√	_ √	√	√	Yes
	plot	X	X	√	1	No
of species	site	X	X	√	√	No
	quadrat	X	X	X	X	Yes
Abundance	plot	X	X	X	X	Yes
	site	X	X	X	X	Yes
Shannon	quadrat	1	V		√ √	Yes
species diversity	plot	X	X	√	_ √	No
	site	X	X	√	 	No
Simpson's	quadrat	7	V	V	V	Yes
species	plot	X	X	√	√	No
diversity	site	X	X	√	V	No

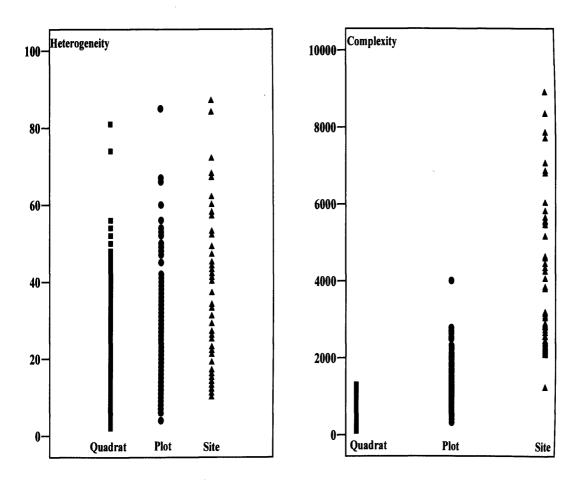
These results indicate that the habitat diversity indices may be used to assess relationships between number of species and species diversity at a grain level of 1m², but not at grain levels of 5m² or 20m².

7.1.4. Relationships across scale: correlations

Abundance and number of species are positively correlated at all grain levels (Table 7.15). Heterogeneity and complexity are not correlated with abundance at any of the grain levels; heterogeneity is scale invariant and values are similar across grain levels, whereas complexity increases with increasing scale (Figure 7.7a). Heterogeneity and complexity are positively correlated with number of species and species diversity only at the 1m² grain level. There are no significant correlations between heterogeneity and number of species or species diversity, nor between complexity and number of species or species diversity, at the 5m² nor 20m² grain levels (Figure 7.7b).

Figure 7.7. The effects of scale on (a) heterogeneity and complexity, and (b) on correlations between heterogeneity and complexity with number of species, abundances and species diversity (Shannon (\log_2) and Simpson's). For (a) data show individual values for quadrats (1m^2 , n=1200), plots (5m^2 , n=240), and sites (20m^2 , n=60). For (b) asterisks indicate significant correlations based on Spearman's rank correlations of number of species, abundances, species diversity and heterogeneity and complexity. For quadrats (1m^2) n=1200, plots (5m^2) n=240, sites (20m^2) n=60 (see Table 6.2 for focus/grain classifications and Table 7.15 for correlation results).

a



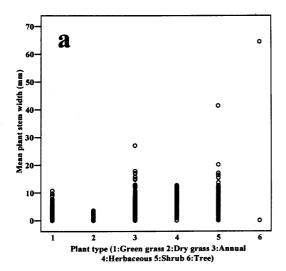
b

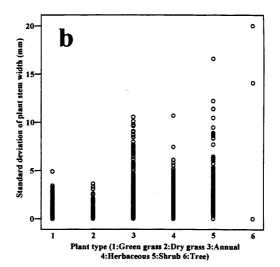
Variables	Quadrat	Plot	Site
Heterogeneity with no. of species	*		
Heterogeneity with abundance			
Heterogeneity with Shannon	*		
Heterogeneity with Simpson's	*		
Complexity with no. of species	*		
Complexity with abundance			
Complexity with Shannon	*		
Complexity with Simpson's	*		

7.1.5. Variation in vegetation: plant stem widths

In general, plant stem widths are less than 20mm. Green grass and dry grass have the narrowest stem widths, and less variation in stem width, than other plant types (Figure 7.8).

Figure 7.8. Plant stem widths from the sites: (a) the mean stem widths, and (b) the standard deviation of stem widths of the six plant types using pooled data from all habitat types and all sites. Each plant type represents data from 1200 quadrats.





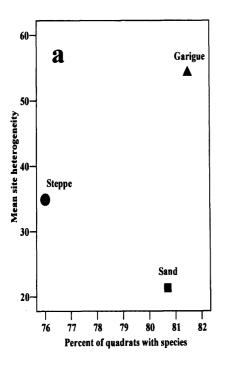
7.1.6. Presence/absence of molluscs in quadrats, plots and sites

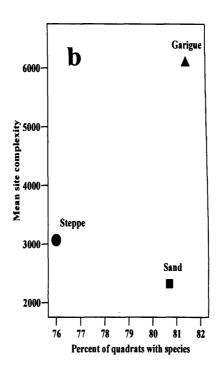
There is an increase in the presence of molluscs with increasing scale (i.e. 1m², 5m² to 20m²), when all sites from all habitat types are considered together, as well as for all habitat type/period combinations (Table 7.17). The number of quadrats and plots at which molluscs were present is not related to total site heterogeneity and complexity at any of the habitat types (Figure 7.9).

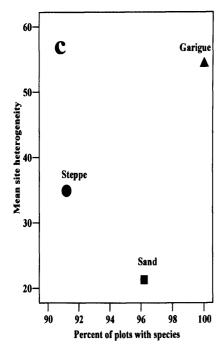
Table 7.17. The number of quadrats (grain: 1m²), plots (grain: 5m²) and sites (grain: 20 m²) at which molluscs were present (with species), and those where molluscs were absent (without species), for all sites, wet sites combined and dry sites combined, and for each of the habitat types (all sites, wet sites and dry sites).

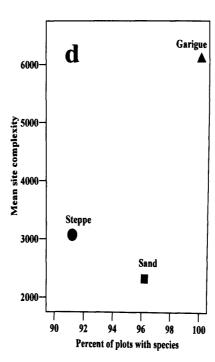
Grain		with	with	without	without
(m ²)	n	species	species	species	species
(111)		n	n as %	n	n as %
			sites		
1	1200	953	79.4	247	20.6
5	240	230	95.8	10	4.2
20	60	60	100	0	0
			t sites		
1	600	469	78.2	131	21.8
5	120	111	92.5	9	7.5
20	30	30	100	0	0
			sites		
1	600	484	80.7	116	19.3
5	120	119	99.2	1	0.8
20	30	30	100	0	0
			VD All sites		
1	400	323	80.7	77	19.3
5	80	77	96.2	3	3.8
20	20	20	100	0	0
10 19		SAN	ND Wet site	es .	
-1	200	159	79.5	41	20.5
5	40	97	93.5	3	7.5
20	10	10	100	0	0
		SA!	ND Dry site	es	
1	200	164	82.0	36	18.0
5	40	36	90.0	4	10.0
20	10	10	100	0	0
		STE	PPE All si	tes	
1	400	304	76.0	96	24.0
5	80	73	91.2	7	8.8
20	20	20	100	0	0
		STE	PPE Wet si	ites	
1	200	149	74.5	51	25.5
5	40	34	85.0	6	15.0
20	10	10	100	0	0
		STE	PPE Dry si	tes	1976
1	200	155	77.5	45	22.5
5	40	39	97.5	1	2.5
20	10	10	100	0	0
		GAR	IGUE All s	ites	
1	400	326	81.5	74	18.5
5	80	80	100	0	0
20	20	20	100	0	0
	20		IGUE Wet	sites	THE LOW
1	200	161	80.5	39	19.5
5	40	40	100	0	0
20	10	10	100	0	0
20	10		IGUE Dry		- 0
1	200	165	82.5	35	17.5
5	40	40	100	0	0
20	10	10	100	0	0
20	10	10	100	U	U

Figure 7.9. The percentage of quadrats (a. and b.) and plots (c. and d.) at which mollusc species were present in relation to mean site heterogeneity and mean site complexity for each of the habitat types (pooled data for each habitat type: n=400 for quadrats, n=80 for plots).









7.1.7. Species estimators

Chao 1 and Chao 2 estimates of numbers of species are similar to the observed numbers of species (Table 7.18, Figure 7.10). In addition, results for Chao 1 and Chao 2 are positively correlated (r_s =0.982, P<0.001, Figure 7.11) indicating that both estimates are producing similar results for the estimates of numbers of species at the sites (Figure 7.12).

Figure 7.10. The number of species from the sites (Observed) with Chao 1 and Chao2. Site 43 had a large number of both singletons and uniques, inflating estimates of number of species by the Chao estimators (see text).

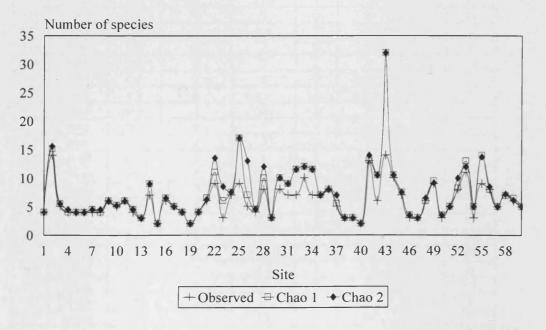


Table 7.18. Estimates of the numbers of species at the sites using the Chao 1 and Chao 2 nonparametric species estimators, showing the observed numbers of species found at each site, the number of species represented by a single individual (singletons: No. sing.), the number of species that occur in only one quadrat (unique species: No. uniq.), and the quadrat at which the species accumulation curves shows an asymptote (Asym.). See Table 6.1 for site details.

Site no.	Habitat type	Period	Observed number of species	Chao 1 estimate	No. sing.	Chao 2 estimate	No. uniq.	Asym.
S1	Sand	Wet	4	4	0	4	0	3
S2	Sand	Wet	14	15.13	3	15.6	4	17
S3	Sand	Wet	5	5.5	1	5.5	1	12
S4	Sand	Wet	4	4	0	4.5	1	19
S5	Sand	Wet	4	4	0	4	0	1
S6	Sand	Wet	4	4	0	4	0	2
S7	Sand	Wet	4	4.5	1	4.5	1	2
S8	Sand	Wet	4	4	0	4.5	0	5
S9	Sand	Wet	6	6	0	6	0	5
S10	Sand	Wet	5	5.25	1	5.25	1	6
S11	Sand	Dry	6	6	0	6	0	11
S12	Sand	Dry	4	4.5	1	4.5	1	4
S13	Sand	Dry	3	3	0	3	0	2
S14	Sand	Dry	7	9	2	9	2	12
S15	Sand	Dry	2	2	0	2	0	3
S16	Sand	Dry	6	6.5	1	6.5	1	5
S17	Sand	Dry	5	5	1	5	1	11
S18	Sand	Dry	4	4	0	4	0	2
S19	Sand	Dry	2	2	0	2	0	4
S20	Sand	Dry	4	4	1	4	1	6
S21	Steppe	Wet	6	6.5	1	6.25	1	12
S22	Steppe	Wet	9	11	2	13.5	3	17
S23	Steppe	Wet	3	6	2	8.5	3	19
S24	Steppe	Wet	7	7.5	1	7.5	1	17
S25	Steppe	Wet	9	17	4	17	4	19
S26	Steppe	Wet	5	7	2	13	4	10
S27	Steppe	Wet	4	4.5	1	4.5	1	6
S28	Steppe	Wet	8	10	2	12	4	15
S29	Steppe	Wet	3	3	0	3	0	4
S30	Steppe	Wet	8	10	2	10	2	5
S31	Steppe	Dry	7	9	2	9	2	9
S32	Steppe	Dry	7	11.5	3	11.5	3	15
S33	Steppe	Dry	10	12	2	12	2	6
S34	Steppe	Dry	7	11.5	3	11.5	3	7
S35	Steppe	Dry	7	7	0	7	0	3
S36	Steppe	Dry	8	8	0	8	0	10
S37	Steppe	Dry	5	5.5	1	7	2	16
S38	Steppe	Dry	3	3	0	3	0	1
S39	Steppe	Dry	3	3	0	3	0	6
S40	Steppe	Dry	2	2	0	2	0	3
S41	Garigue	Wet	13	13.1	1	14	2	12
S42	Garigue	Wet	6	10.5	3	10.5	3	20
S43	Garigue	Wet	14	32	6	32	6	20
S44	Garigue	Wet	10	10.5	1	10.5	1	17
S45	Garigue	Wet	7	7.5	1	7.5	1	19
S46	Garigue	Wet	3	3.5	1	3.5	1	7
S47	Garigue	Wet	3	3	0	3	0	17

Table 7.18. (continued).

Site no.	Habitat type	Period	Absolute number of species	Chao 1 estimate	No. sing.	Chao 2 estimate	No. uniq.	Asym.
S48	Garigue	Wet	6	6	0	6.5	1	. 3
S49	Garigue	Wet	9	9.5	1	9.17	1	16
S50	Garigue	Wet	3	3.5	1	3.5	1	11
S51	Garigue	Dry	5	5	0	5	0	10
S52	Garigue	Dry	8	8.25	1	10	2	9
S53	Garigue	Dry	11	13	2	12	2	19
S54	Garigue	Dry	3	5	2	5	2	10
S55	Garigue	Dry	9	14	5	13.75	5	20
S56	Garigue	Dry	8	8	0	8.5	1	15
S57	Garigue	Dry	5	5	0	5	0	10
S58	Garigue	Dry	7	7	0	7.25	1	16
S59	Garigue	Dry	6	6.5	1	6.17	1	3
S60	Garigue	Dry	5	5	0	5	0	3

Figure 7.11. Chao 1 estimated number of species versus Chao 2 estimated number of species. (Spearman's=0.982, P<0.001).

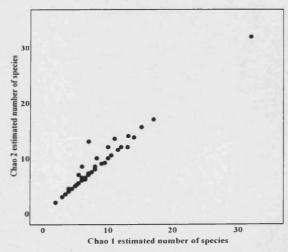
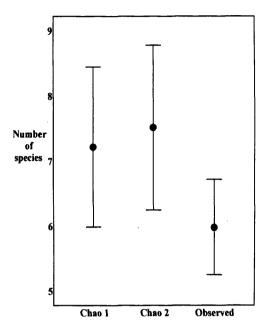


Figure 7.12. The number of species estimated by Chao 1 and Chao 2, and the observed number of species. Markers indicate the mean, and upper and lower crossbars the 95% confidence levels of the mean.



7.1.8. Species accumulation curves

The quadrat at which an asymptote is attained for the accumulation curves is related to the number of species at the sites (Table 7.18), with asymptotes being attained at higher numbers of quadrats, the more species are present at a site (r_s 0.530, P<0.001). Asymptotes were not attained at three sites, and five sites attained asymptotes by Quadrat 19 (Table 7.18). These results indicate that sampling further quadrats may have increased the species inventories at these sites.

7.1.9. Summary of results

The results are summarized below (and see Table 7.19):

- 1. There was a mean number of six species at the sites, with a mean total species abundance of 358.7, a mean Shannon diversity of 1.443, and a mean Simpson's diversity of 0.516.
- 2. There were more species in the wet than dry period at sand and garigue habitats (at the three grain levels), but in the steppe habitat there were more species in the dry, than the wet, period. Combining all sites (wet and dry), the habitat types order from lowest to highest for number of species as: (1) sand, (2) steppe, (3) garigue.
- 3. Abundances were higher in the wet than in the dry period at sand and steppe habitats (at the three grain levels), but abundances were higher in the dry, than the wet, period in garigue. Combining all sites (wet and dry), the habitat types order from lowest to highest for abundances as:

 (1) steppe, (2) garigue, (3) sand.
- 4. Shannon and Simpson's diversities were higher in the wet than in the dry period at sand and garigue habitats (at the three grain levels), but diversity was higher in the dry than the wet period in steppe. Combining all sites (wet and dry), the habitat types order from lowest to highest for diversity as: (1) sand, (2) steppe, (3) garigue.
- 5. Increased heterogeneity is associated with a higher number of species but is not associated with higher species abundances.
- 6. Increased complexity is associated with a higher number of species but is not associated with higher species abundances.

- 7. Some components of habitat structure (principal structures) positively affect the number of species and species abundances independently of total complexity whilst others negatively affect both parameters.
- 8. The number of species, species abundances and species diversity increase significantly as spatial scale increases.
- 9. At the 1m² level of grain, heterogeneity and complexity are positively associated with increased number of species and species diversity, but not with species abundances.
- 10. Combining all sites (wet and dry), the habitat types order from lowest to highest for heterogeneity and complexity as: (1) sand, (2) steppe, (3) garigue.
- 11. Heterogeneity and complexity are greater in the wet period than the dry period.
- 12. Combining all sites (wet and dry), the habitat types order from lowest to highest for variation in heterogeneity as: (1) garigue, (2) steppe, (3) sand, and for variation in complexity as: (1) sand, (2) garigue, (3) steppe. There is generally more variation in both heterogeneity and complexity in the wet period than in the dry period at all habitat types.
- 13. There are significant differences in heterogeneity and complexity for all habitat types.
- 14. There are significant differences in heterogeneity and complexity for many habitat/period combinations, but there were no differences for wet and dry periods at steppe (heterogeneity), and wet and dry periods at sand, and wet and dry periods at steppe (complexity).

- 15. Heterogeneity and complexity are positively correlated at all grain levels.
- 16. Habitat diversity indices may be used to assess relationships between number of species and species diversity at a grain level of 1m², but not at grain levels of 5m² or 20m².
- 17. Relationships between heterogeneity, complexity, number of species and species diversity are scale-dependent.
- 18. In general, plant stem widths are less than 20mm with grass having the narrowest widths, and less variation in width.
- 19. There is an increase in presence of molluscs with increasing scale (i.e. $1m^2$ to $20m^2$), from 79.4% to 100%, respectively.
- 20. There is an increase in the presence of molluscs with increasing scale (i.e. 1m² to 5m² to 20m²), when all sites from all habitat types are considered together, as well as for all habitat type/period combinations.
- 21. The number of quadrats and plots at which molluscs were present is not related to total site heterogeneity and complexity.
- 22. There is a positive correlation between Chao 1 and Chao 2 estimated number of species and the observed number of species.
- 23. Results for Chao 1 and Chao 2 are positively correlated.
- 24. Asymptotes in species accumulation curves are attained at a higher number of quadrats the more species are present at a site.

Table 7.19. Summary of the hypotheses tested indicating acceptance or rejection.

Hypothesis number	Description	Analyses	Accepta Reject (A/R)
H_1	The higher the heterogeneity, the more species present	Spearman's correlation of heterogeneity with number of species	A ¹
H_2	The higher the heterogeneity, the higher the abundances of species	Spearman's correlation of heterogeneity with abundances of species	R ²
H_3	The higher the complexity, the more species present	Spearman's correlation of complexity with number of species	A^3
H_4	The higher the complexity, the higher the abundances of species	Spearman's correlation of complexity with abundances of species	R ⁴
H_5	Some types of heterogeneity affect number of species independently of total complexity	Partial correlations between variable pairs, whilst holding total complexity constant	A
H_6	Some types of heterogeneity affect abundances of species independently of total complexity	Partial correlations between variable pairs, whilst holding total complexity constant	A
H ₇	The number of species increases as spatial scale increases	ANOVA	A
H_8	The abundances of species increases as spatial scale increases	ANOVA	A
H_9	There is more variation in heterogeneity in some habitat types than in others	Coefficient of Variation (CV) of heterogeneity ⁵	A
H ₁₀	There is more variation in complexity in some habitat types than in others	Coefficient of Variation (CV) of complexity ⁵	A
H ₁₁	Heterogeneity differs between the habitat types	ANOVA	A
H ₁₂	Complexity differs between the habitat types	ANOVA	A
H ₁₃	Heterogeneity differs between the wet and dry periods at each habitat type	ANOVA	A
H ₁₄	Complexity differs between the wet and dry periods at each habitat type	ANOVA	A
H ₁₅	Heterogeneity differs between the wet and dry periods between the habitat types	ANOVA	A
H ₁₆	Complexity differs between the wet and dry periods between the habitat types	ANOVA	A

¹Rejected for sand (all sites), sand (dry sites).

³Rejected for sand (dry sites), steppe (dry sites).

See Section 7.1.2 for discussion of reasons for 1 to 4.

²Accepted for sand (all sites), sand (wet sites), steppe (all sites, wet sites, dry sites).

⁴Accepted for sand (all sites, wet sites, dry sites), steppe (all sites, wet sites), garigue (all sites, dry sites).

 $^{^5}$ The CV is used to assess variation of heterogeneity and complexity from sites. The analysis does not enable significance testing and so, strictly, this is not a formal statistical testing of the hypotheses. The decision to accept/reject the hypotheses is based on the values of CV for the habitat types (see Tables 7.1 to 7.8, and 7.13 to 7.15, and text for further details).

7.2. Discussion

7.2.1. The number of species, abundances and diversity

The data from Part Two of this study were collected to determine the effects of habitat structure and scale on the diversities of land molluscs (Section 1.5) using sampling methods and scales that differed from those used in Part One (Sections 3.5.1 and 3.5.2) where the sampling aim was to maximize species inventories at sites. As a result comparisons cannot be made between the species data from Parts One and Two, nor to those from other studies that have sampled plots of similar size to those of Part Two (e.g. Tattersfield, 1996; Cameron *et al.*, 2003; Lange and Mwinzi, 2003). These other studies have mostly sampled molluscs over the entire area of the plots, generally of 1600m². In this study an area of 20m² was sampled for each 40x40m site, representing 1.25% of the total area of the site (Chiarucci *et al.*, 2003), and 1.25% of the total area sampled in other studies. Furthermore, soil (generally 4-5 litres) was collected from sites in studies that aim to maximize species inventories (Section 3.5.2, Table 3.4), whereas soil was not collected from sites in Part Two of this study.

7.2.2. Heterogeneity and complexity

Increased heterogeneity and complexity are associated with a higher number of species, but not with higher species abundances. Recent work with algal fronds and gastropod assemblages (Kelaher, 2003b), and amphipods in Australian rocky shores (Schreider *et al.*, 2003) have shown no, or negative, associations between complexity and the number of species and abundances.

By determining the number of species, heterogeneity and complexity are also determinants of community composition (Walla *et al.*, 2004). The increase in number of species with higher heterogeneity and complexity support other

studies that have demonstrated this relationship for other taxa including birds (Hurlbert, 2004), marine macroinvertebrates (Edgara *et al.*, 1994), copepods (Hicks, 1980), marine gastropods (Jones and Boulding, 1999), freshwater macroinvertebrates (Buss *et al.*, 2004) and marine benthic communities (Jacobi and Langevin, 1996). Recent studies of Mediterranean isopods have shown that the number of species is proportional to habitat heterogeneity, and may also affect community structure (Gentile and Argano, 2005).

There is greater variation in heterogeneity than complexity at the habitats indicating that sites of the same habitat types vary in how many different types of structure they include, but that there is less variation between sites in the quantity of overall structure these represent. Variation in heterogeneity is not correlated to variation in complexity, indicating that some types of structure may contribute to variation in complexity to a lesser or greater degree at some habitats than others. Vegetation, for example, may contribute more to variation in complexity than quantity of rocks. Biotic variables, such as vegetation and leaf litter, may therefore increase the inherent variability in habitats more than abiotic variables such as rocks and stones.

7.2.2.1. The habitats

Thirty-nine species were recorded from steppe habitat sites, 39 from garigue habitat sites and 17 species from sand habitat sites (Appendix 10). Sand habitats, therefore, have less than 50% of the number of species that steppe and garigue habitats have, and lower species diversity. The species present at sand sites include those that constitute the Sand malacofaunal group identified in Part One (Section 4.2.2.2).

Both heterogeneity and complexity increase from sand through to steppe to garigue. Sand is the least heterogeneous and least complex habitat, and has greatest variation in heterogeneity, but least variation in complexity. Complexity is related to resource availability (e.g. food and shelter resources) and this habitat may be more predictable in terms of providing resources for land molluscs. In addition, the decrease in available resource types in this habitat, in comparison to steppe and garigue, may result in species that are better adapted to using them out-competing those that are less well adapted. This may partly explain the high abundances of some of the species that occur (see below).

In steppe and garigue there is less variation in heterogeneity, but more variation in complexity. This is the opposite of the finding for sand and indicates that steppe and garigue habitats have less variation in the number of resources they provide to land molluscs, but that the quantity of these resources is more variable and thus less predictable. Such habitats may support more species (May, 1984; Schopf and Ivany, 1998), and this may explain why there are more species and higher diversities in steppe and garigue than in sand.

Sand habitats provide less habitat structure than either steppe or garigue habitats. This probably limits the number of species found. Some species, such as *C. acuta*, *X. apicina* and *T. pisana*, whilst present in steppe and garigue, are principally associated with sand habitats. Although sand habitats have less species and lower diversity than steppe and garigue habitats, species abundances are generally higher than in the other habitats. Three possible explanations are:

(1) that species such as *T. pisana* and *C. acuta* may have adaptations that allow them to use this habitat type efficiently (Arad and Arivi, 1998; Arad *et al.*,

1993; Kempster and Charwat, 2003). These two species aestivate on vegetation and other habitat structures during the dry period where aggregations, or 'herds' of snails may include both species, with *C. acuta* occupying spaces between the shells of *T. pisana*.

Snails in aestivation are in a period of temporal refuge from external conditions that buffers them against disturbance (Giokas *et al.*, 2007, and see Widenfalk and Solbreck (2005) for a similar situation with gall midge larvae in soil). Aggregations may provide benefits to individuals at high population densities by diminishing risk of attack from enemies, or by providing a density-dependent spatial refuge against predators (Hunter, 2000; Rohlfs and Hoffmeister, 2004). There is evidence from this study that some individuals do not remain attached to the aggregates throughout the dry period. Observational data (unpublished) show that some individuals become active during late evening to early morning, and move both on vegetation and on the sand substrate. Furthermore, these individuals are generally those situated at the peripheries of aggregations. This strategy, that has not been reported before in southern Iberia, probably has cost-benefit implications (Calow, 1984; Krebs, 1985) and may increase fitness (Christiansen, 1984; Sibly and Calow, 1985).

A different strategy for living in sand habitat is used by *X. apicina*. This species does not use the upper strata of vegetation. Instead it remains at ground level and in the 10cm stratum (unpublished data). It also forms aggregations, generally at the bases of plants, but remains active through most of the year, moving on vegetation and on the sand substrate during late evening to early morning.

- (2) the low number of species in this habitat type may decrease interspecific competition which, via competitive release, may account for the higher abundances of species present (Faeth, 1984; Grant and Schluter, 1984; Jutila and Grace, 2002). Evidence for competitive release in land mollusc communities is, however, limited (Barker, 2005). Hatziioannou *et al.* (1994) reported that *Monacha cartusiana* (Müller, 1774) in Greece showed competitive release in using a larger area of the habitat during winter when other species were hibernating. Barker and Mayhill (1999), on the other hand, did not find evidence for competitive release in communities from Pukeamaru scrublands and forests in New Zealand.
- (3) Theba pisana and C. acuta may not depend on cover for predator avoidance, and so may avoid habitats with high structural complexity (Lima, 1993; Elkin and Baker, 2000; Hill et al., 2004). Most studies in this area centre on vertebrates and insects, and Hill et al. (2004) showed that praying mantids selected habitat of less complexity which facilitated predator avoidance and foraging ability. There are many predators of land molluscs including insects, birds, reptiles and mammals (reviews in Barker, 2004) but no published data from southern Iberia exist. The author's unpublished data show that insects, principally Lampyridae, predate on Sphincterochila spp., Xerosecta spp., Iberus spp., Theba spp., Otala spp., E. vermiculata, and C. aspersus. There is also evidence for predation from rodents and reptiles (unpublished data).

Steppe and garigue habitats include widespread species identified in Part One (and which constitute the Universal malacofaunal group, Section 4.2.2.2). The organization of species assemblages in communities result from two main processes: niche-assemblage (species adapted to niches determines organization,

following deterministic processes) and dispersal-assembly (localized dispersal events and demographic stochasticity, following stochastic processes) rules (Jenkins and Buikema, 1998; Hubbell, 2001; Hardy and Sonké, 2004) and differences in numbers of species and their abundances in the different habitats may be partly related to these processes.

Data from this study do not support the More Individuals Hypothesis (Srivastava and Lawton, 1998) which states that areas with greater food resources support more individuals, and communities with more individuals include more species. Instead, the data largely support the Resource Specialization Hypothesis (Pianka, 2000) which suggests that as productivity increases (in the more complex steppe and garigue habitats), the number of resource types that can support specialist species (from this study examples include Oestophora spp., Ponentina subvirescens (Bellamy, 1839) and Psuedotachea litturata (Pfeiffer, 1851)) increases, and niche apportionment models that assume that the distribution and availability of niches in a habitat determine the relative abundance of species filling the niches (Tokeshi, 1999; Hutton and Giller, 2004; Stubbs and Wilson, 2004). Barker and Mayhill (1999), for example, have reported that mollusc diversity and abundance may be regulated by niche availability where sites of high vegetation diversity have higher fractal complexity and more microhabitat differentiation than sites of low vegetation diversity.

The presence of some species at all habitat types (e.g. C. lenticula, O. lactea, and C. aspersus) suggests that these have wide tolerances to habitat structural characteristics, microclimatic effects, predation risks and the food resources these habitats present. Very little is known of the food preferences of

the majority of land snails (Speiser, 2001; Lydeard et al., 2004), although there is evidence that good quality food may be a limiting factor at certain times of the year for some species (Carter et al., 1979). Food availability may not be a determinant factor for species diversity between habitats because most land molluscs are microphagous, feed on live and decaying vegetation (Speiser, 2001; Martin and Sommer, 2004), and occur in a range of different habitats where completely different food types are available. In addition, some species may eat a completely different diet at different places (Speiser, 2001).

7.2.2.2. The sampling periods

Variation in heterogeneity and complexity is greater in the wet than in the dry period, subjecting land molluscs to greater overall habitat structure variability during the most active parts of their life cycles, including periods of egg-laying and hatching. This may be an important determinant of the number of eggs produced and survival of individuals, and so of land mollusc abundances in these habitats.

Heterogeneity and complexity are generally higher in the wet period than in the dry period and increased plant growth in the wet season may partly explain this. More species were recorded in the wet period than in the dry period at all habitat types. During the wet period there is an increase in land mollusc activity, and therefore movement of individuals within the habitat space. This increases dispersion and so the probability of finding species in any given area. Inactivity during the dry period, on the other hand, results in aggregation of individuals in the habitat space, decreasing the probability that they will be detected by a sampling method that relies on random, or semi-random, quadrat sampling (Section 8.1). Spatial aggregation may occur even in homogeneous

habitat patches (Bohan et al., 1997, 2000). This effect could be measured using a greater number of quadrats at the sites and analyzing spatial distribution (Section 8.5) during the wet and dry periods.

Abundances were higher in the wet period in sand and steppe habitats reflecting the increase in juvenile and sub-adult individuals (data not presented) from previous egg hatching events during the wet period. In the heterogeneous and complex garigue habitat there is a reverse in this trend, with abundances being higher in the dry, than the wet period. The ratio of abundance in wet:dry periods is markedly different for the three habitats (see Table 7.1 for data). The ratio for sand and steppe is 1.8 and 2.4, respectively, but 0.5 for garigue. Observational data from this study (not presented), as well as unpublished data, indicate that there are no differential activity patterns among species in garigue, in comparison to sand and steppe, during the wet and dry periods.

Possible explanations for the reverse trend in abundances between the garigue, and the sand and steppe habitats include: (1) the differential use of habitat components by species in the different habitats. Some species, for example, may be present in the soil/leaf litter during different parts of the year and, (2) predation on land molluscs in the habitats may follow different processes and dynamics. de Winter (1995), however, was not able to differentiate between wet and dry sites using species data from a rain forest in Gabon, western Africa. The differences found in species data from this study suggest that seasonality may be an important determinant factor of land mollusc diversity in southern Iberia.

7.2.3. Habitat structure

7.2.3.1. Vegetation and plant stem widths

Plant communities in the Mediterranean region are highly diverse with high total and local species richness, and high spatial heterogeneity (Lavorel, 1999; Sternberg and Shoshany, 2001; Alados et al., 2004; Fernández et al., 2004) and isolated patches of vegetation are a key element for community structure and dynamics in semi-arid ecosystems (Maestre and Cortina, 2005). The results from this study show that there is considerable variability in vegetation at sites, both in the height and coverage attained by plants, as well as in the variability in stem widths. Vegetation varies considerably in species composition, diversity, in the plant types represented (grass, herbaceous, shrub etc.) and in their components (stem, leaf etc. see Appendix 8), both within and between sites. Many studies have shown that plant communities determine the physical structure of the environment, providing the habitat template for the assembly of animal species in multi-trophic communities (Tews et al., 2004; Tscharntke and Hawkins, 2004). In this study vegetation comprises a significant proportion of the habitat structure at many sites (Section 7.1.2) and impacts significantly on number of species and their abundances (Section 7.2.3.2). Variation in plant structural components may influence movement and dispersion in habitats. Grasses, for example, have less variance than annuals and herbaceous species (assessed using stem widths, Section 7.1.5). Further research, however, is required to test this hypothesis.

7.2.3.2. Habitat structure and principal structures

The data from this study show that the presence of some types, or components, of structure affects the number of species and abundances of land molluscs, independently of the total quantity of structure (i.e. of total complexity). These results support those of Beck (2000) who reported that the effects of heterogeneity on the number of species and abundances of rocky intertidal gastropods in Botany Bay, Australia, were independent of complexity.

Some components of habitat structure were positively associated with number of species and species abundances, whilst others were negatively associated with these. These associations were generally neither habitat nor sampling period specific, and components may have different effects (positive or negative) at different periods and in different habitats types. The results show that, although generalizations regarding the importance of habitat components for land molluscs (e.g. leaf litter, vegetation types) may hold across a range of habitats, there are nonetheless some differences among habitats. The results further suggest that the effects of habitat components on the number of species and abundances of land molluscs may be determined by both the habitat type and season.

Ground level components, such as leaf litter, shingle, stones and rocks are of particular importance to land molluscs (Waldén, 1981; Luchtel and Deyrup-Olsen, 2001), and species such as *F. folliculus* and *C. lenticula* are mostly found in this part of the habitat, and often in high abundance in relation to other species. Rocks provide cover for many land molluscs and are associated with species not commonly found in other parts of the habitat (e.g. *Cecilioides* spp.).

Large rocks may provide shelter for some species during the dry period when temperatures under small rocks, stones and on the ground surface can exceed 50°C (unpublished data); temperatures under embedded and large non-embedded rocks are lower than those on the ground surface, and moisture levels are higher. Species that are active on the vegetation during the wet period (e.g. *Iberus* spp., *O. lactea* and *C. aspersus*) are often only found under large rocks during the dry period (unpublished data), and *F. folliculus* and *C. lenticula* that are found under shingle and stones (see above) may shelter preferentially under large rocks when these are available. Recent work by Moreno-Rueda (2002, 2006, 2007) in southern Iberia has shown that *Iberus gualtieranus gualtieranus* (Linnaeus, 1758) uses rock fissures for refuges and that its shell morphology may be adapted for easier access to these fissures. Rocks have also been reported to be a shelter requirement for snails in desert habitats (Dillon, 1980).

Land molluscs have poor dispersal abilities (Cook, 2001; Russell-Hunter, 1983; Section 8.4) that are affected by habitat factors such as type and height of vegetation, population densities and time of year (Greenwood, 1974; Cameron and Carter, 1979; Boag and Wishart, 1982; Cain, 1983; Cowie, 1984; Baker and Hawke, 1990) as well as types of rocky habitat (Baur and Baur, 1994). Similar factors affect dispersal abilities in spiders and insects (Crist *et al.*, 1992; Cartar and Real, 1997; McNett and Rypstra, 2000).

Land molluscs are dependent on features of habitat structure and these may be a limiting factor for many of these species in some habitats (see below). Shelter may only be limiting in the dry months, but this would still be expected to have effects on populations, and abundances, throughout the year (Stewart-Oaten and Murdoch, 1990). If some species are limited in this way then those

species are expected to have lower abundances than species that are not limited. This may partly explain the higher abundances of species such as *T. pisana* in relation to *C. aspersus* where they occur together, and the finding that, in general, there is a positive association with habitat heterogeneity and complexity with number of species, but not with their abundances.

Other Mediterranean land molluscs, especially slugs, are limited by conditions during the dry period and may only be found during the wet period (Cameron et al., 2003; Section 3.5.1), remaining buried in soil, or under large rocks, during the dry period. Temporal scale has been shown to affect the types of factors that influence collembolan communities (which have similarly low dispersal abilities) in tree stumps, and as the temporal scale is reduced from an annual to a seasonal one, micro-habitat, rather than macro-habitat factors become determinant (Setälä et al., 1995). In addition, Ritchie and Tilman (1992, 1993) showed that grasshoppers exhibited interspecific competition only if plant biomass was reduced significantly. These facts suggest that intra- and interspecific competition in land molluscs in these habitats is not for food resources (which are in abundance) but for one, or very few, physical structures (heterogeneity types) of the habitat (Baur and Baur, 1990). Experimental work involving the provision of refugia (artificial or natural) in delimited areas of habitat space would provide data on the dependence of land molluscs on key components of habitat structure (such as rocks and logs). These experiments would require temporal and spatial aspects of the habitat systems to be controlled and would represent a novel approach in determining land mollusc diversity-habitat structural effects to be assessed.

Intra- and interspecific competition are, however, very difficult to demonstrate (Connell, 1980; Chesson and Warner, 1981; Strong, 1984; Wise, 1984; Atkinson and Shorrocks, 1991; Palmer, 1992; Crowley *et al.*, 2005), and there is controversy on their relative importance in structuring communities (McIntosh, 1985; Kitching, 1986; Underwood, 1986; Arthur, 1987). The evidence for competition as a factor regulating land mollusc communities is weak and generally inconclusive (Mordan, 1977; Solem, 1984b; Cowie and Jones, 1987; Nekola and Smith, 1999). Cameron *et al.* (2000), for example, indicate that evidence for competition in limiting local diversity in Aegean land snails is sparse. Evidence for competition has also been found to be inconclusive for other invertebrate taxa (Horton and Wise, 1983; Wise, 1984). Ward and Lubbin (1993), for example, considered competition not to be an important factor in habitat selection by desert spiders.

No competition was detected between endemic and non-endemic mollusc faunas in Madeira (Cook, 1984), the author suggesting that non-endemics add to the number of species already present. Simberloff (1981) showed that introduced species generally did not produce recorded change in community persistence, although there is evidence that *Cernuella* (*Cernuella*) *virgata* (Da Costa, 1778) may be excluded by *T. pisana* in coastal sites in South Australia (Smallridge and Kirby, 1988).

Gittenberger (1984) suggested that lack of competition in the ancestral taxa of *Chondrina* has allowed species migration. Barker and Mayhill (1999), however, suggest that the relationship between vegetation diversity and species diversity in northeastern New Zealand forests may indicate that assemblages are structured around niche partitioning among competing species (Diamond, 1975;

Stubbs and Wilson, 2004), but their evidence is circumstantial. Millar and Waite (1999) found a negative correlation between diversity and abundance in an English wood, and suggested that as abundance increases the community becomes dominated by a limited number of species, and that the decrease in diversity might result from competition. There is some evidence for intra- and interspecific competition for *Cepaea* (Tilling 1985a, 1985b).

There are very few reported cases of competition in Mediterranean land molluscs. Magnin (1993) and Labaune and Magnin (2001) demonstrated competition between *Trochoidea geyeri* (Soós, 1926) and *Candidula unifasciata* (Poiret, 1801) along altitudinal gradients in southeastern France, and Hausdorf (2001) showed competition effects between vitrinids and limacoid slugs.

The lack of, or reduced effects of, competition have raised the possibility that there may be vacant niches (Lawton, 1984) in land mollusc faunas. Cameron (1988) suggested that incomplete convergence of forest snail faunas from northwest Europe and British Columbia may indicate the existence of empty niches. He also reported that all niches seemed not to be filled in the fauna of the Madeiran archipelago (Cameron, 1992). More recently, Barker (2005) reported that lack of constancy in richness in most bioregions in New Zealand suggests either that not all species have yet reached all suitable sites, or that there is marked spatial heterogeneity in environmental quality and thus availability of niches. He concluded that New Zealand land snails are not at equilibrium with the contemporary environment and that spatial heterogeneity in the landscape, coupled with as yet incomplete saturation of suitable niches, contributes to the patterns of highly varied site occupancy and turnover in species richness.

A vacant niche signifies that all points on the resource axis of the resource utilization function (MacArthur, 1968) are available for use, but that not all are used (Arthur, 1987). To identify a niche as vacant, it is necessary to know that the niche could potentially sustain a population, and evidence for vacant niches can mostly be provided by comparisons with analogous communities (Srivastava et al., 1997). Local communities and patches may be unsaturated, saturated or super-saturated with species; however, species range boundaries settle to a pattern of geographical overlap and many species are constrained well within their fundamental niche (Brown et al., 1996; Whittaker et al., 2001). There may be significant underestimation in the number of vacant niches in many ecological communities (Srivastava et al., 1997) but much more data are required to determine if there are vacant niches in land mollusc faunas in southern Iberia.

The presence of rocks was positively associated with number of species at sand and steppe, but not garigue habitats. Lack of association in garigue is attributed to the rocks being mostly embedded, or forming a part of rocky outcrops (data not presented) in many of the quadrats in this habitat (in contrast to rocks at sand and steppe that were mostly not embedded). This results in molluscs probably not being able to use the areas under rocks, and also prevents sampling under these rocks. The lack of association may also be because structural components are not limiting to diversity in garigue to the same extent as in sand and steppe. Further evidence for this is that leaf litter is not associated with number of species at garigue, but is at sand and steppe.

Other studies have reported positive associations with diversity and quantity of litter for land molluscs (Locasciulli and Boag, 1987; Barker and

Mayhill, 1999; Millar and Waite, 1999, 2002; Kappes, 2005; Kappes *et al.*, 2006) and other taxa (Mazía *et al.*, 2006). The distributional patterns of molluscs in litter are complex (Locasciulli and Boag, 1987; Barker and Mayhill, 1999; Barker, 2005) and detailed sampling of litter would be required to elucidate more fully relationships between land molluscs and litter (Kuźnik 1997) (Section 8.5).

Virtually all terrestrial systems are founded on soil (Fitter, 2005) and fauna is an important part of soil environments (Cortet *et al.*, 1999; Salmon *et al.*, in press). Many studies have demonstrated the importance of soil in determining diversity and structuring the communities of many taxa (Xiong and Nilsson, 1999; Fioretto *et al.*, 2003; Larchevêque *et al.*, 2005; Johnson *et al.*, 2006; Kappes *et al.*, 2006; Decaëns *et al.*, 2006) including land molluscs (Cameron, 1986; Sólymos, 1996; Sólymos and Nagy, 1997; Kiss and Magnin, 2003). Studies from Iberia have also demonstrated the importance of soil in determining diversity and structuring land mollusc communities (Hermida *et al.*, 1995; Ondina *et al.*, 1995, 2004). In this study, soil was negatively associated with number of species at sand and steppe, and no positive associations were found at any of the habitats.

Soil was considered to be a component of habitat structure, and quadrats with large quantities of soil (mostly from sand and steppe sites) had lower heterogeneity and complexity (Appendix 13). Other than surface searching, soil was not sieved for land molluscs. Based on findings for soil sampling from Part One, soil from sites in Part Two would have contained individuals that were not recorded in this study, especially in steppe and garigue where some of the smaller species that were recorded on the ground and lower vegetation layers

(e.g. *F. folliculus*, C. *lenticula* and *X. conspurcata*) are also present in soil (unpublished data). Soil sampling would allow relationships between soil and land molluscs to be assessed, and this type of sampling would therefore be an improvement to this study (Section 8.5).

Grasses and annuals in the garigue habitat are associated with number of species and abundances, indicating that these may be important resources to land molluscs in habitat that is vegetationally complex but that has many plant species that may not be edible. Heller (1988) showed that in semi-arid environments snails prefer annual plant debris over perennial plants which are difficult to eat or digest. The data from this study, and in particular those from garigue habitat, support this and show that, in general, grasses and annuals are of particular importance to land molluscs but that the other plant types are less so. This suggests that some of the plant types, such as the annuals and grasses, may be preferred food items over shrubs and some herbaceous plants that contain high levels of ethereal oils, released to reduce water loss and minimize herbivory (Polunin and Walters, 1985). Compounds in plant tissues including terpenoids, phenolics and caffeic acid esters have been shown to be herbivory deterrents for many molluscs (Rice et al., 1978; Harborne, 1982).

The present study also indicates that vegetation may provide resources to land molluscs that are used in different ways in the three habitats. In all habitats, shrubs and/or trees are negatively associated with number of species and abundances, supporting the suggestion that these may be non-edible by land molluscs (see above). Herbaceous plants, most of which are also probably inedible, are negatively associated with number of species only in garigue. In sand and steppe, however, they are positively associated with both number of

species and abundances. This plant type provides the principal sites for aestivation for species including *T. pisana* and *C. acuta* in these habitats, and these species occur at much higher densities in sand and steppe than in garigue. The results suggest that this plant type is important in providing shelter (during aestivation) rather than as a food resource, and support findings by Kiss and Magnin (2003) that non-edible plants provide litter and shelter for Mediterranean snails.

According to Boycott (1929, 1934), in general neither quantity nor quality of a plant food source influences snail distribution. Similarly, Russell-Hunter (1964) suggested that vegetation affects the distribution of land molluscs through its modification of microclimate (Section 5.3), but that land molluscs are not associated with particular plant species as food plants. Peake (1978) has also stated there is no evidence that palatable vegetation is a limiting factor for land molluscs. Although it is not clear if land mollusc populations are food limited, results from this and other studies (Carter *et al.*, 1979; Baur and Baur, 1990; Speiser, 2001) suggest they may be in some circumstances.

Structures, such as rock, that may be more important in affecting number of species and abundances than others are termed 'principal structures'. Tews et al. (2004) have recently introduced the concept of 'keystone structures' that is almost analogous to the 'principal structures' proposed here. They define a keystone structure as: '...a distinct spatial structure providing resources, shelter or 'goods and services' crucial for other species.... For example, dead wood in mixed beech-spruce forests may be a keystone structure.' They report strong correlations of beetle diversity with the within-habitat heterogeneity of vegetation structure. Discontinuities in species-accumulation curves are used to

indicate the presence of keystone structures, which requires a continuous gradient (measured along a transect). In the method used in this study partial correlations are used with other variables to identify principal structures, removing the need to use transects (as in Tews *et al.*, 2004) and so allowing the identification of these structures from quadrat data.

There are currently insufficient data to ascribe conclusively the causes of observed spatial heterogeneity in land mollusc communities in southern Iberia. Both environmental and biotic factors are, however, probably important as proposed by the two main models that describe the spatial heterogeneity observed in plant and animal communities. These are the environmental control model, where environmental variables cause variation in presence or abundance of organisms, and the biotic control model, where links among organisms such as competition and predation structure communities (Borcard *et al.*, 1992).

7.2.3.3. Measures of habitat diversity

The positive correlation between heterogeneity and complexity at all levels of grain suggests that habitat diversity indices may be used to assess the effects of habitat structure on number of species and species diversity. This is because heterogeneity and complexity comprise the two components of habitat diversity indices (in the same way that number of species and abundances comprise the two components of species diversity indices). Heterogeneity and complexity are two of the axes of McCoy and Bell's (1991) 3-dimensional habitat structure model (the other is scale, Section 5.3), and using habitat diversity indices reduces the model to two dimensions (habitat diversity and scale). The data from this study support this use only for 1m² (quadrat). The results indicate that

there may be a scale-dependent relationship that may determine the use of habitat diversity indices.

7.2.4. Scale effects

A major consideration in assessing the relationship between habitat structure and the number of species and abundances is the scale at which this relationship is measured (McCoy and Bell, 1991; Dutilleul, 1993; Miguel *et al.*, 2005). Although there are recently published studies on land mollusc diversity from delimited sampling areas (Section 5.2) these have not specifically considered the data from the same locations at varying scales.

In a detailed assessment of the number of species in Cretan maquis undertaken at the scales of 1x1km and 20x20m (the site and plots within it) Cameron et al. (2003) highlighted the need for this work: '... our results from Cretan maquis show a very high level of homogeneity between plots; the grain of the environment is such that most, if not all, significant elements of the habitat can be found in a single plot and, when they are present, they are occupied. We have no doubt, though it requires verification, that at much smaller scales this would cease to apply, and there would be much greater variation in richness and composition between plots.'

Animal species respond to their environment at different spatial scales (Ray and Hastings, 1996; Gehring and Swilhart, 2003) and to study the response of animals to their habitat, variables need to be measured at a scale appropriate for the animal and phenomena under study (Waide *et al.*, 1999; Ludwig *et al.*, 2000; Holland *et al.*, 2004). Species characteristics, such as body size and dispersal in the habitat, have been used to explain the scale at which species respond to their environments and if the habitat is not adequately defined from

the organism's viewpoint any detected relationships between the organism and the habitat are weakened (With and Crist, 1996; Holland *et al.*, 2005).

Using inappropriate scales can cause the researcher to arrive at the wrong conclusions about the relationships between species and habitat (Hanski, 1987). Pearce (2002), for example, reported a positive correlation between land snail diversity and patch size from eastern USA. This correlation was lost on adding further sites (Pearce, 2003) indicating that land snails were not conforming to island biogeography and species-area theories (MacArthur and Wilson, 1967; MacArthur, 1972; Cox and Moore, 1985; Section 5.2). Pearce (2002) reports that other studies have similarly not found positive correlations and also provides the most probable reason for his lack of positive correlations, and by extrapolation, those of others, (Pearce, 2003). These reasons centre on scale, with Pearce's patches of 300 hectares probably being too large to assess the response of land snails to patch size and fragmentation (Bevers and Flather, 1999; Krawchuck and Taylor, 2003; Chust *et al.*, 2004).

This study's results indicate that relationships between heterogeneity, complexity, number of species and species diversity are scale-dependent. Most of the statistically significant relationships between these occur at the smallest grain level (1m²). Increasing the grain to 5m² and then 20m² results in these relationships being lost. Relationships between land molluscs and habitat structure are therefore only detectable at this small scale and this relates to the way molluscs perceive and operate in the habitat (Section 8.4). There is evidence that ecological processes among other invertebrate taxa may only be detectable at very small scales and relationships may be lost if scale is increased (Mazía et al., 2006). Heads and Lawton (1983), for example, found that a leaf-

miner parasitoid aggregated strongly in areas of high host density and that the effects of spatially density-dependent mortality of the host were present at scales of 0.03m^2 , but was not detectable at 1m^2 .

Most ecosystems exhibit extreme heterogeneity in environmental conditions and biotic communities at multiple spatial scales (Heino *et al.*, 2004) and recent studies have shown that extreme environmental heterogeneity exists across gradients, such as intertidal gradients, previously assumed to be relatively monotonic (Sagarin *et al.*, 2006). The findings from this study suggest that assessing land mollusc diversity/habitat structure relationships needs to be carried out at scales that are far smaller than those usually employed (Cameron *et al.*, 2003).

7.2.4.1. Presence/absence of molluscs in quadrats, plots and sites

Molluscs were present at all sites and at most of the plots at all sites. Presence at quadrats ranged from 74.5 to 82.5% (Table 7.17) indicating that molluscs are dispersed throughout most of the habitat. Sampling for molluscs was efficacious (Section 6.5) and the assumption is that the non-detection of molluscs in some quadrats indicates absence. Because leaf litter and soil were not sieved for specimens it is possible that there may have been specimens in this part of the habitat that were not detected. This would be expected to increase the number of quadrats with the presence of molluscs, and represents a limitation of the sampling method.

There were more quadrats and plots at which molluscs were present in sand than in steppe, and this may be because species such as *T. pisana* and *C. acuta*, may be more widely dispersed, and have higher abundances, in sand than in steppe. In garigue there were more species than in sand or steppe, and the

presence of molluscs at a greater number of quadrats may reflect this higher richness as well as wider dispersion of molluscs in the habitat.

The results are similar for wet and dry periods at each habitat indicating that the habitats are being used in a similar way (as regards occupation) in both periods. This interpretation may be too simplistic, however, because abundances during the two periods at the habitats suggest that there is differential use of habitat components during the year (Sections 7.2.2.2 and 7.2.3.2), at least in garigue (where abundances were higher in the dry period). Dispersion in the habitats, related to random and non-random use of habitat components and aestivation sites, cannot be detected by assessing the presence of individuals in quadrats and plots. This is because finding even one individual would classify the quadrat or plot as having the presence of molluscs.

The utilisation of habitat structure and dispersion of molluscs in the habitat space can be assessed by mapping the positions of individuals in the quadrats, calculating dispersion indices in a similar way to dispersion in larger areas and determining temporal change in these (Brower *et al.*, 1989; Cox, 1990; Menez, 2001). This is a research priority in Mediterranean habitats where different conditions in wet and dry periods of the year may determine the use of habitat structure by molluscs.

7.2.5. Estimation of the number of species and sampling issues

Chao 1 and 2 both gave estimates that were close to the observed number of species at the sites, indicating that the sampling method used was efficacious. The positive correlation between the two measures shows that either could be used for the type of data from this study.

The species estimators could not be used for sites from Part One (Section 4.1.1) because the estimators assume homogeneity amongst the samples (i.e. site similarities) (Section 4.1.1). An improvement to the approach used in this study would be to sample a number of sites (of the size used in Part One) of different habitat types across southern Iberia, and to use the species estimators. Comparing the findings with those using the site sizes and layouts from Part Two would allow the assessment of both sampling efficacy and estimator efficacy at two very different scales of measurement.

The accumulation curves suggest that full species inventories may not have been achieved at some sites. This finding mostly applies to sites that have more species (in general these were garigue sites). This, in conjunction with the results for the species estimators, suggests that a higher number of quadrats are needed to sample some of these sites adequately (Anne Chao, *pers. com.*). Although each individual quadrat may be sampled adequately (Section 6.5), this study's findings suggest that the number of quadrats required to sample an area effectively is dependent on how structurally complex the habitat is, and how dispersed the individuals are in the habitat.

7.2.6. Species-area effects

The increase in the number of species with increase in area sampled (i.e. grain level) supports the species-area model (MacArthur and Wilson, 1967; Rosenzweig, 1995; Section 5.2) and is an example of the species-area relationship with nested sampling areas of increasing size (Rosenzweig, 1995; Scheiner 2003; Crist and Veech, 2006). The number of species, abundances and species diversity increased with increasing area, while heterogeneity and complexity were uncorrelated with these, except at the 1m² grain level.

Furthermore, complexity increased with increasing area, while heterogeneity did not. These findings indicate that heterogeneity and complexity cannot explain the increase in number of species with increasing area and thus the habitat diversity hypothesis is rejected as an explanation for the species-area relations from this study. These results support those of Nilsson *et al.* (1988) who found that in Swedish islands the number of land mollusc species increased with area, but that habitat diversity was uncorrelated with area.

The increase in abundances with increasing area sampled supports the passive sampling model (Section 5.2), the increase in number of species with increasing area in this study may result from samples that contain greater numbers of individuals. The species-area relations from this study, therefore, are explained by the area *per se* hypothesis (Section 5.2), and not the habitat diversity hypothesis (see above). This result reflects a fundamental pattern in nature where larger samples, whether of molecules, regions of the universe or ecological communities, contain a greater diversity of their fundamental elements (Lomolino and Weiser, 2001).

7.3. Summary of Part Two

Sixty sites, each 1600m², were sampled in southern Iberia. 20 sites were located in each of three habitat types (sand, steppe and garigue), and for each habitat type ten sites were sampled in the wet period, and ten sites in the dry period. A stratified, nested design was used at each site to select four plots each of 25m², at which five quadrats of 1m² were sampled; diversities and habitat structure were assessed at 1m², 5m² and 20m². There was a mean number of six species at the sites (lower 95% CI: 5.26; upper 95% CI: 6.74) with a mean total species abundance of 358.67 (lower 95% CI: 247.26; upper 95% CI: 470.07), a mean

Shannon diversity of 1.443 (lower 95% CI: 1.282; upper 95% CI: 1.603) and a mean Simpson's diversity of 0.516 (lower 95% CI: 0.464; upper 95% CI: 0.568). (Table 7.1, Figure 7.1).

There were differences in the number of species, abundances and diversities between habitats and between the wet and dry periods at each habitat. The number of species was lowest in sand and highest in garigue; abundances were lowest in steppe and highest in sand, whilst diversity was lowest in sand and highest in garigue. Increasing heterogeneity and complexity increased the number of species, but not their abundances. Components of habitat structure affected the number of species and abundances independently of the total complexity.

The number of species, abundances, and diversity increased with increasing scale, while heterogeneity and complexity were uncorrelated with these, except at the 1m² grain level. Relationships between heterogeneity, complexity, number of species and species diversity were scale-dependent with most of the statistically significant relationships between these occurring at 1m². Heterogeneity and complexity were greater in the wet period than the dry period, and there were significant differences in heterogeneity and complexity for all habitat types; the habitat types order from lowest to highest for these as: (1) sand, (2) steppe, (3) garigue.

The increase in abundances with increasing area sampled supports the passive sampling model with the increase in number of species with increasing area resulting from samples that contain greater numbers of individuals. These species-area relations support the area *per se* hypothesis.

CHAPTER 8. GENERAL DISCUSSION

Iberia is one of the regions in Europe with highest species diversity and endemism (Bellés, 1990; Ramos *et al.*, 2001). Its varied topography has provided suitable habitats through several glacial cycles allowing the divergence and accumulation of genomes (Knowles, 2001; Branco *et al.*, 2002). Southern Iberia was not covered by the Pleistocene ice sheets (Narciso *et al.*, 2006) and was a main refugium during this epoch (Carrión *et al.*, 2003; Habel *et al.*, 2005). There has, therefore, been a longer time period in southern Iberia, in relation to other regions such as mid- and northern Europe, for biotic communities to develop, for the promotion of speciation and for species diversity to increase (Knowles, 2001; Ribera and Vogler, 2004).

This study's findings support this interpretation of Iberia and show high regional diversity for land molluscs (Gamma diversity of 4.05), a high degree of differentiation, or turnover in species composition (Beta diversity: 7.77), and a mean number of species at sites (12.1; lower 95% CI: 11.2; upper 95% CI: 13.0) in the mid-range by global standards (Cameron *et al.*, 2000). The malacofauna of southern Iberia, in being diverse with many endemics, shares characteristics with other Iberian faunas, with Mediterranean faunas in general, and with some eastern European faunas (Wells and Chatfield, 1992, 1995).

Relationships between heterogeneity, complexity, number of species and species diversity are scale-dependent. Most of the statistically significant relationships recorded in this study occur at the smallest grain level (1m²). Increasing the grain to 5m² and 20m² results in these relationships being lost. Relationships between land molluscs and habitat structure are only detectable at this smallest scale and this relates to how molluscs perceive and operate in the

habitat. There is evidence that ecological processes among other invertebrate taxa may also only be detectable at very small scales and relationships may be lost if scale is increased (Mazía *et al.*, 2006).

There may be two principal levels at which explanatory factors for the distribution and diversity of land molluscs in southern Iberia may be sought: large-scale factors that include climate, habitat types as well as colonization histories of habitats, and small-scale factors such as habitat heterogeneity and complexity. These may broadly be considered as regional and local factors (Griffiths, 1999; Gaston, 2000; Whittaker *et al.*, 2001; Herzog and Kessler, 2006), respectively. Any model explaining distribution and diversity would need to account for both these factors. The effects of these two factors have received considerable attention (Ricklefs, 1987; Borcard *et al.*, 1992; Cornell and Lawton, 1992; Hugueny and Cornell, 2000; Arita and Rodríguez, 2002) and two main, and related, conclusions have been that the availability of suitable habitats at the regional scale determines local species abundances (Irmler and Hoernes, 2003), and that focusing only on local processes might not reflect patterns and processes underlying diversity relationships in communities (Cardinale *et al.*, 2004).

8.1. Sampling issues

Different studies have different aims, and sampling methods differ depending on these aims (Magurran, 2004; Cameron and Pokryszko, 2005). In Part One the main aims of this study were to provide a preliminary biogeographical survey of the land molluscs of southern Iberia, and to determine the factors that affect their distribution and diversities in the region (Sections 1.5, 3.4 and 3.5). In Part Two the aims were to assess the effects of habitat heterogeneity and complexity

on the number of species and species abundances at three scales, in three habitat types, and to determine whether these effects are scale-dependent and habitat-specific (Sections 1.5, 6.4 and 6.5).

The strength and nature of species-environment relationships, for communities as well as for individual species, can differ significantly between analyses using presence/absence versus abundance data (Cushman and McGrail, 2004). In this study abundance data have generally been used for assessing the relationships between species and environmental data, both for the biogeographical and habitat structure analyses.

In Part One sites were selected to encompass as much habitat variation as possible (Section 3.2), and sampled using direct search and soil/litter collection techniques (Sections 3.5.1, 3.5.2). Cameron and Pokryszko (2005) advocate the use of both direct search and litter sampling, and Emberton *et al.* (1996) reported that direct searching yielded about 75% of total species in a plot. Cameron and Pokryszko (2005) concluded that for greatest efficiency in assessing the number of species, direct sampling should be carried out in conjunction with litter and soil sample collection. In 1km² sites up to 20% of species may be missed if soil and litter sampling are not included (Menez, 2007). Part Two aims required random assignment of quadrats at sites (Section 6.4) with associated detailed sampling of the quadrats for land molluses and the recording of environmental variables (Sections 6.5 and 6.6).

This study used both main approaches for sampling land molluscs: that for maximizing species inventories, and that for assessing effects of environmental variables on diversity. For either approach to provide reliable ecological information, sampling must be as rigorous as possible (Bishop, 1977;

Menez 2001, 2002a). Inefficient sampling will result in underestimates of local richness, even in favourable habitats (Cameron *et al.*, 2006). It is, however, almost impossible to census a community completely. Instead samples are taken and some form of extrapolation is carried out to estimate the number of unobserved species (O'Hara, 2005). Absence of species in samples does not imply they are not present in the locality (Waldén, 1981), and in some cases a definitive answer as to whether or not an abnormally low diversity is real can only be given after extended sampling, in some cases over several years. Single-visit surveys cannot give complete species inventories (Cameron and Pokryszko, 2005) and this limitation is recognized in this study (Section 8.5).

Rarity of species needs to be considered in relation to sampling methods. Sampling macroinvertebrates reveals only a part of the community at a site because species present in low abundance have a lower chance of being sampled than species with high abundance (Nijboer and Schmidt-Kloiber, 2004). The number of individuals, and relation between this and number of species, are important in determining the accuracy of species' estimates (Cameron and Pokryszko, 2005). Hayek and Buzas (1997) recommend a minimum of 200-500 individuals, and Cameron and Pokryszko (2005) a ratio of individuals to species of about 10:1. These recommendations cannot always be met, especially at low-density sites. Caution is therefore necessary in the interpretation of diversity in these situations, with the probability of failing to detect a species increasing as densities fall (Cameron, 1986). This is illustrated by data from tropical rainforests where the number of species tends to be high but difficult to assess because of low densities (Emberton *et al.*, 1996).

Collecting effort and sampling error (de Winter and Gittenberger, 1998; Walther and Moore, 2005) are two other main factors that impact on the accuracy of inventories and information about variation in samples. Emberton *et al.* (1997), for example, reported that much of the variation in samples from Tanzania seemed to be the effect of collecting effort. Sampling error, defined by Cameron and Pokryszko (2005) as the failure to find a species in a quadrat, site or area when it is actually present, may obscure patterns among species (Swan, 1970).

The advantages of quadrat (as used in Part Two) over qualitative sampling for land molluscs far outweigh the extra time involved (Bishop, 1977), with quadrat sampling providing information about spatial dispersion and allowing precision levels to be set on population estimates in the measurement of inter-site differences. Quadrat sampling gives unbiased estimates of density and occurrence, and data from different sites can be compared. It is, however, inadequate for assessments of species inventories (Emberton, 1995b), for two main reasons (see Cameron and Pokryszko, 2005): (1) species abundances and distributions make quantitative sampling inefficient (in particular for large species, and for slugs) and, (2) seasonal variation in densities and microdistribution of species (in particular of small to medium-sized species). Including fresh dead shells can reduce the problems of using quadrat and volume methods, by increasing sample size and overcoming some of the seasonal variation (Cameron and Pokryszko, 2005). Very little is known about shell degradation rates and the factors that affect these (Section 4.5.3). The findings of this study, as well as those of Menez (2001), support the use of methods from Part One for inventory work.

Sampling error (see above) may be small when quadrats are searched exhaustively (Cameron and Pokryszko, 2005), as in this study. When an unbiased sample is taken from a community where individuals are randomly distributed the chances of finding or missing a species are determined by the absolute size of the sample, and the relative frequency of that species (Magurran, 2004; Cameron and Pokryszko, 2005). Most plants and animals are not randomly distributed in habitats (Southwood, 1978; Inouye, 1999) and this is true for land molluscs that may be present in aggregations (Cameron and Pokryszko, 2005).

The two main approaches for sampling land molluscs (maximizing species inventories and assessing effects of environmental variables on diversity) raise issues of collector objectivity and subjectivity. Objective statistical treatment of sampling data generally demands that random methods are used in selecting sample areas. These areas include quadrats, plots and sites, and every area for sampling must have an equal probability of being selected (Section 6.4.1). This requirement for randomness completely removes input from the researcher in selecting which specific area is to be sampled, although including criteria for the initial selection of sites (Section 6.2) and using a stratified design (Section 6.4.1) allows the selection of appropriate habitats to be used.

An alternative approach is often used for the collection of inventory data, where the aim is to maximize the number of species recorded from a locality. This approach considers that use should be made of information, obtained from previous or pilot surveys, about the nature of the underlying spatial structure of the variables (Legendre *et al.*, 2002), and that familiarity of

the study area and taxa under investigation increase the chance of finding individuals (Greenwood, 1996). The experience and knowledge of the researcher in selecting appropriate microhabitats and areas of the habitat to sample preferentially therefore becomes an important factor in the collection of species data. The use of random sampling and researcher familiarity in assessing species and environmental data was highlighted by Kikkawa (1986): 'Comparison of complex communities cannot easily be based on replicate samples, with known statistical properties. The more familiar one becomes with complex communities, the more sceptical one grows about the validity of random sampling in estimating habitat features or abundance of organisms'.

An overlooked effect of sampling, whether or not it considers spatial and/or temporal replication, is that the very act of sampling itself affects the results. This is akin to the Heisenberg Principle in physics, and the observer effect (or observer bias) in science generally, which describe changes that the act of observing have on the phenomena being observed (Robertson, 1929; Hawking, 1988; Davies, 1992). Examples in land mollusc sampling are: (1) the collection of environmental data, as in this study, will disrupt the sampling area, and so may alter the probability of finding individuals (which for rare species represented by one or two specimens, means the species may not be recorded at all) and, (2) the handling or removal of individuals may impact a population, especially of rare species. Crushing individuals underfoot whilst sampling, the extent of which may not even be known by the researcher, could change community dynamics. Chappell *et al.* (1971), for example, reported that trampling reduced the population densities of some land molluscs in a chalk grassland. This study has shown that some species, especially large ones such as

Iberus spp., may be present at low density: destroying one or two may represent the entire plot's population. These events may be considered to be stochastic events, in the way that animals may remove individuals, by predation or trampling, or in the way a rock may fall from a hillside and destroy a whole colony of *Theba*. Complete randomness in sampling is almost impossible to achieve.

8.2. Diversity indices

Two indices of species diversity were used: Simpson's index (Ds), and the Shannon index (H') (Sections 3.7.1.3 and 6.9.1.3). These two indices are commonly used in ecological studies and they allow comparisons of data. The Shannon index is more sensitive to sample size, whereas Simpson's index provides a good estimate of diversity at relatively small sample sizes (Magurran, 2004). Results for both indices were comparable when used with species data from both the 1km^2 sites from Part One (Figure 4.1), as well as the much smaller areas sampled in Part Two (Figure 7.1). This indicates that, in this study at least, either of the indices may be used to describe species diversity.

8.3. The habitat structure model

Heterogeneity and complexity are positively correlated at all grain levels, but combining the two into habitat diversity indices results in correlations at only the 1m² grain level. These findings suggest that habitat structure, and the effects of this on land molluscs, are best considered using the three components of the McCoy and Bell (1991) model (Figure 8.1).

8.4. The land molluscs' perspective

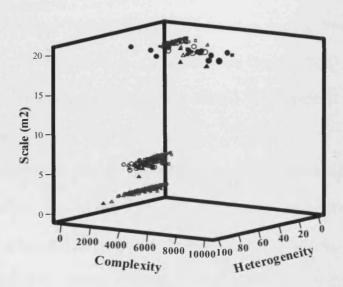
One of the main findings of this study is that habitat structure correlates with species data at a very small scale. Many positive correlations were found at 1m², but these were lost at 5m² upwards. This highlights how land molluscs may be operating at scales very different to the ones they are usually studied at (Boycott, 1934; Cameron and Pokryszko, 2005), and how the definition of habitat for different species depends on the spatial scale of perception of each species (Nilsson *et al.*, 1988; Mech and Zollner, 2002; Miguel *et al.*, 2005).

Nekola and Smith (1999) sampled land molluscs from Wisconsin cliff communities at 1m² and 0.04m², and suggested that resource levels at these scales may be high. They did not, however, assess environmental factors at these scales so it is not possible to compare the results of this study to their data. These workers reported that the high richness of land snails in carbonate cliff habitats is present to very limited spatial scales. Up to 62% of site richness (and up to 22% of state richness) were found within single 0.04m² areas along cliff bases. Data from this present study seem to support both their findings and the prediction of Cameron et al. (2003) that relationships between land mollusc diversity and environmental factors may be different at these small scales in comparison to the scales at which these relationships are usually assessed. In addition, Barker and Mayhill (1999) reported that most New Zealand molluscs are confined to the litter on the forest floor, which is probably the primal habitat of land molluscs. Litter is a highly complex, three-dimensional, horizontally stratified habitat that, from the snail's perspective, is divided into many subunits: newly fallen leaves at the top, fragmented leaves, twigs, and

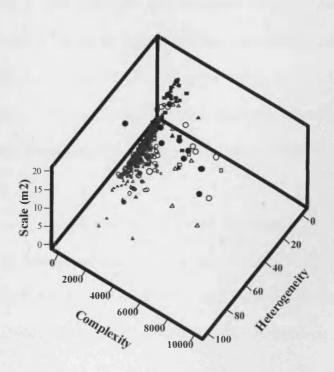
decomposed litter at intermediate levels, and wet litter and then particulate humus at ground level.

Figure 8.1. Three-dimensional plots of scale, heterogeneity and complexity. (a) normal view and (b) bird's eye view. For each plot the data are shown for the three grain levels and are individual values for each level (quadrats, 1m^2 , n=1200; plots, 5m^2 , n=240; sites, 20m^2 , n=60). Habitat types: sand=circular markers, steppe=square markers, garigue=triangular markers.

a



b



Aubry et al. (2005) reported that the patterns observed for species richness in land snails in southeast France depended on the scale of resolution, with richness controlled by many factors, operating at different scales on individual species. Similar results have been reported for other taxa: work with littoral zone communities has shown that species that are uncommon and highly aggregated at coarse spatial scales can be abundant and approach random distributions at finer spatial scales (Stoffels et al., 2003), and work with beetles has shown that they respond to habitat at scales ranging from 20 to 2000m (Holland et al., 2004). Similarly, Langellotto and Denno (2004) showed that, for arthropods, habitat structure varies from simple to complex at several relevant spatial scales.

The landscape forms a hierarchy that contains thresholds in object sizes and proximities, and textures at particular scales, with the smaller scales dominated by vegetative processes (Archibald, 1949; Holling, 1992; Grossi *et al.*, 2004; Hall *et al.*, 2004). An animal's perceptual range is the fraction of the landscape that is both detectable and accessible via movement, and so defines the spatial scale at which an individual interacts with the landscape (Olden *et al.*, 2004; Patterson *et al.*, 2007). Perceptual range may be limited by factors such as vision, olfaction, body size and resource requirements (Mech and Zollner, 2002; Fleishman *et al.*, 2003; Schooley and Wiens, 2003; Zollner and Lima, 2005).

Species may perceive environments as being either heterogeneous or homogeneous based on the relationship between body size and habitat heterogeneity, with resultant effects on diversity and abundance (MacArthur and MacArthur, 1961; Morris, 1987; Holling, 1992; Rosenzweig, 1995; Wiens et

al., 1995). Perception of, and reaction to, environment is also related to life-history characteristics including resource requirements, and taxonomic groups vary in their responses to environmental patterning, including the spatial and temporal distribution of biotic and abiotic resources (Levin, 1992; Straw and Ludlow, 1994; Davidowitz and Rosenzweig, 1998; Fleishman et al., 2003). The seed beetle Callosobruchus maculatus (Fabrricius, 1775) (Coleoptera, Bruchidae), for example, responds to the sizes of seeds available and oviposit on larger seeds when the heterogeneity of seeds is increased (Yang et al., 2006). Farji-Brener et al. (2004) reported that the interaction between the spatial distribution of food resource and environmental grain influenced the match between resources and tropical litter ants, and that the efficiency in food resource exploitation by ant species with different body sizes was directly related with the scale of environmental heterogeneity.

Kawata et al. (2001) reported considerable variations in filamentous algal abundance between and within stones in streams, and Kawata and Agawa (1999) showed that freshwater snails recognize algal patches as heterogeneous when patch size is 25 to 50mm long. They also found that spatial scales smaller than 25mm determine the behaviour of grazers as well as the spatial heterogeneity of the algae. There is evidence for bacterial patchiness at scales below 1mm, further demonstrating the relationship between organism size and operational scale (Dechesne et al., 2003; Nunan et al., 2003).

The relationship between scale and diversity is likely to differ among taxa in relation to mobility (Hamer and Hill, 2000). The decisions that animals make when selecting a habitat affect the ecological interactions they are involved in, their morphology, and the selective pressures that shape their

genotypes and those of their descendants (Davis and Stamps, 2004; Milner and Vonesh, 2004). Many arthropods, including spiders and wasps, use structural features of the habitat as cues for settling in an area of the habitat (Ward and Lubin, 1993; Collett and Zeil, 1998). Additionally, theoretical models suggest that habitat selection by any mobile animal should reflect a balance between costs and benefits to organism fitness accruing from the use of alternate habitat types (Langkilde and Shine, 2004).

How individuals move in the habitat influences the probability they will experience physiological stress, encounter potential mates, prey or predators (Wiens et al., 1995; Michel et al., 2007). The ability of animals to move on a wide array of substrates may be critically important for various ecological tasks including predator escape, thermoregulation and finding mates (Vanhooydonck et al., 2005). As movement pathways are influenced by habitat structure, they may reflect differences in how organisms perceive habitat heterogeneity over different scales (Kotliar and Wiens, 1990; Johnson et al., 1992; Nams, 2005). Movements should follow the structure of the environment, exhibiting, for example, an increase in turning rate and decreased speed where resources are plentiful (Benhamou, 2004; Pinaud and Weimerskirch, 2005). Coarser typologies and scale are suitable when analysing highly mobile species. Species with small movement ability, such as land molluscs, perceive more detail, and a finer typology and smaller scale is appropriate (Suárez-Seoane and Baudry, 2002).

Land molluscs generally remain in a small area of habitat and can actively disperse only up to a few metres per year within it (Schilthuizen and Lombaerts, 1994; Hausdorf and Henning, 2003). Baur and Baur (1993) found

that *Arianta arbustorum* (Linnaeus, 1758) covered a median distance of 0.58m in 24 hours, and Parmakelis and Mylonas (2004) reported a maximal monthly dispersion distance for released *Mastus* of less than 4m. *Theba pisana* released into pasture fields have been shown to have mean dispersal distances of less than 7m (Baker and Hawke, 1990), and Giokas and Mylonas (2004) reported a mean dispersal distance of 1.62m for *Albinaria coerulea* (Rossmässler, 1835). Mobility even for larger species is not great, and Tomiyama and Nakane (1993) found that adult *Achatina fulica* (Bowdich, 1822) moved an average of 1.5m per day.

This, and other studies, have shown that there are differences in the spatial distribution of land molluscs in habitats (Section 8.1). At the small scales at which many land molluscs operate, these differences may result from some species not being able to colonize all suitable habitat because they cannot reach isolated fragments (Johansson and Ehrlén, 2003; Matlack and Monde, 2004). Any species that lacks the ability to disperse is greatly exposed to extinction risks (Paradis, 1998). Whitehouse *et al.* (2002) found that large-scale environmental factors influenced coarse-grained community structure in spiders, whilst small-scale differences between patch types resulted in the specialisation of species to the different patch sizes.

Habitat Selection Theory emphasizes the ability of species to disperse and colonize patches with the highest expected fitness, with resulting distribution patterns being a function of the spatial redistribution of individuals among patches (Morris, 2003; Binckley and Resetarits, 2005). This may partly explain the non-random distributions of land molluscs at various scales.

8.5. Improvements to this study: future research

The following are identified as potential improvements to this study:

- 1. Increasing the number of sites sampled: For Part One it would have been better to have sampled a greater number of habitat types per site. This would have allowed the analysis of habitat type effects (as was done in Part Two) at the biogeographical scale.
- 2. Replication: Although replication can be difficult in large-scale ecological studies (Hurlbert, 1984; Carpenter, 1990), Part One of this study could be improved by carrying out replication of sampling and environmental data collection at the sites. Pseudoreplication is frequently a problem with many ecological studies and adequate replication design would be required to avoid this (Hurlbert 1984, Heffner et al., 1996; Oksanen, 2001).
- 3. Correlations: The sequential Bonferroni adjustment, introduced by Holm (1979), could have been used in the analyses of correlations because of the large number of calculations carried out (Neuhäuser, 2004), although there are numerous arguments against using this adjustment in ecological and other studies (Rothman, 1990; Perneger, 1998; Moran, 2003; García, 2004). With 100 comparisons, five correlations with a P of <0.05 are expected even in the absence of real effects (Chandler, 1995; Rae, 2004). Where many correlations with a P of <0.05 are obtained, as in this study however, it is reasonable to conclude that the majority of these correlations are of real significance (Townsend $et\ al.$, 1987).
- 4. Spatial analysis: Spatially based sampling typically shows spatial dependence as a result of nearby quadrats being, on average, more similar to each other than distant ones (Eberhardt and Thomas, 1991; Lechowicz and Bell,

1991; Palmer and White, 1994; Fortin and Dale, 2005). Autocorrelation is an observed feature in much spatially sampled biological data (Augustin et al., 1996; Sokal et al., 1998; Xu et al., 2005) that can lead to problems identifying possible relations between biotic and abiotic factors (Legendre and Fortin, 1989; Dale et al., 1991). Environmental patterns that are very complex over small areas are probably very common in nature and spatial data analysis can be used to assess these (Phillips, 1985; Legendre, 1993; Heikkinen et al., 2004; Jetz et al., 2005). Species richness depends greatly on the spatial distribution of species. Hoyle (2005) found that micro-arthropods in fragmented communities, which suffer reduced species richness, are more aggregated both within and among habitat patches. The influences of habitat complexity, climate and topography vary spatially and species distribution patterns change with spatial resolution in response to these variables (Buckly and Roughgarden, 2005). Further data could be collected to assess spatial effects using spatial and autocorrelation techniques (Dungan et al., 2002; Perry et al., 2002; Fortin and Dale, 2005; Rangel et al., 2006).

5. Analysis of nestedness: Nestedness is one of the most commonly observed properties of a regional collection of local biotas (Cook, 1995; Cook and Quinn, 1995; Gaston and Blackburn, 2000) and perfect nesting occurs when species-poor sites contain subsets of the assemblages found in species-rich sites (Hausdorf and Henning, 2003; Fischer and Lindenmayer, 2005; Wethered and Lawes, 2005). Nestedness is a multi-scale phenomenon (Cook et al., 2004) and the amount of nestedness quantifies the degree of overlap in species composition between low and high diversity sites (Wright et al., 1998; McAbendroth et al., 2005). Hausdorf and Henning (2003) have reported that the

ranges of northwest European land snail species are significantly nested, and that differences in the degree of nestedness are mainly due to differences in the variance of range sizes and not dispersal abilities. Hylander *et al.* (2005) have reported significant nestedness in land molluscs in Swedish forests and that variation in environmental variables among sites can result in nested communities. There are no data for southern Iberia in relation to nestedness and this study could be improved by collecting data from additional sites and assessing nestedness.

- 6. Temporal analysis: Extending the sampling from this study over several years would allow analysis of inter-year patterns in species diversities (Pahl-Wostl, 1991; Virkkala, 1991; Basset et al., 2001).
- 7. Collection of molluscs from soil at the habitat structure sites: Although soil and litter were sampled for land molluscs at the Biogeographical Sites (Part One), this was not carried out for the Habitat Structure Sites (Part Two) where the aim was to assess the effects of habitat heterogeneity and complexity on the number of species and species abundances at small scales. In some cases soil sampling may be the only way to detect some species (Lee, 1993; Oggier et al., 1998). It is possible, therefore, that soil may have contained individuals that were not recorded in this study, and including soil sampling would allow relationships between soil and land molluscs to be assessed at these small scales.

Cameron and Pokryszko (2005) state that: 'One of the major challenges in the ecology and biogeography of terrestrial molluscs is to determine the scales at which patterns of distribution occur, and the extent to which they correlate with environmental variation at small scales'. Many unanswered

questions remain in land mollusc ecology and there is potential for much original research, examples are:

- 1. How do relationships between diversity and environmental factors operate over differing scales?
- 2. How do species interact with environmental structures (such as rocks, logs and soil) in different habitat types? Are these interactions universal, or do they differ biogeographically? (Section 7.2.3.2).
- 3. How do temporality and seasonality impact on relationships between diversity and environmental variables?
- 4. What are the food preferences (in particular, of plant types) of land molluscs in southern Iberia? Do some plant species affect diversity as a result of use by land molluscs as food resources, or as refugial components of habitat structure?

In addition there is scope for investigating experimentally the responses of different land molluscs to habitat heterogeneity and complexity. Perea *et al.* (2007), for example, assessed the effects of light and substratum complexity on microhabitat selection by *C. aspersus*, using similar methods to those used by Menez (1996) with the marine gastropod *Stramonita heamastoma* (Linnaeus, 1766).

Part Two of this study has assessed the effects of habitat heterogeneity and complexity on the number of species and species abundances at three discrete scales: 1m², 5m² and 20m², but there are no data available about effects when scale is considered as a continuum. It is probable that these effects may not always be linear (Fleishman *et al.*, 2003; Kelaher, 2003b) and there may be thresholds in habitat heterogeneity and complexity that affect species diversity.

In addition, these effects may change in direction and magnitude (Gotceitas and Colgan, 1989; Kelaher, 2003b). This may define the minimum quantities of heterogeneity and complexity that are associated with varying levels of number of species and abundances in the habitats. Upper thresholds may exist, and increasing heterogeneity and complexity beyond these may have no effect on number of species and abundances, or may negatively impact on them. The present data show that thresholds should occur between 1m² and 5m², and this defines the scale at which associations between land molluscs and habitat structure are occurring (Section 8.4) (although correlations were low to modest (Chapter 7) and further work is required to better define associations). The habitat structure model (Section 8.3) would allow the data to be analyzed in this way if data were collected along a scale continuum, and analyzing these data in this way would be a novel approach in land mollusc ecology.

8.6. Concluding remark

The publication *Pattern and process in land mollusc diversity* (Cameron *et al.*, 2005a), and other papers presented at the Third World Congress of Malacology in Perth, Western Australia (July 11-16, 2004), update the analyses made by Solem (1984b) about global patterns of land mollusc diversity. These are summarized by Cameron *et al.* (2005b) as: (1) the number of species from good sites varies little between regions, except at extreme high latitudes, at metacommunity or regional level, the number of species is greater at low latitudes; (2) metacommunity richness and morphological range vary idiosyncratically between regions, and are often related to historical and phylogenetic factors, topography and nature of the habitat. Regions affected by Pleistocene extinction are poor at regional, but not local level; and, (3)

biogeographical patterns in land molluscs are unusual because of the large number of restricted endemics present in many regions.

Cameron et al. (2005a) is the first collection of papers on land molluscs where issues of scale take prominence in attempts to understand land mollusc diversity. This, and other recently published papers, highlight that this is a topical area of research. Cameron and Pokryszko (2005) stated that determining the scales at which distributional patterns occur and the extent to which they correlate at small scales with environmental variation is a major challenge in land mollusc ecology. In addition, Brown (1999), Lawton (1999) and Scheiner et al. (2000) have identified that moving from pattern to process is one of the great challenges facing ecology today. This study is centred in these areas of research and will be built on over future years in an attempt to better understand pattern and process in southern Iberian land mollusc diversity.

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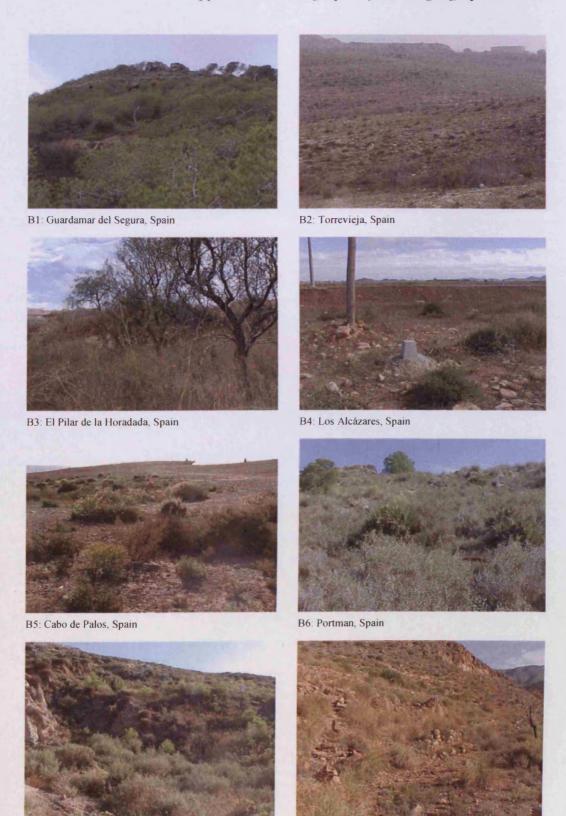
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Appendix 1. The numbers of species (No. Spe), total abundances (Total Abund), Shannon diversity (base 2 logs) and Simpson's diversity at the Biogeographical Sites, showing sampling dates and the latitude and longitude of each site (measured in minutes and degrees).

Site	Ct. N	T	Ī	I	No.	Total	Shannon	Simpson's
No.	Site Name	Date Sampled	Latitude	Longitude	Spe	Abund	Diversity	Diversity
B1	Guardamar del Segura, Spain	30/10/2000	3804698	00039537	15	1473	2.925	0.816
<u>B2</u>	Torrevieja, Spain	30/10/2000	3800642	00040219	16	2181	2.733	0.804
B3	El Pilar de la Horadada, Spain	31/10/2000	3752200	00047617	15	2189	1.893	0.579
B4 B5	Los Alcázares, Spain Cabo de Palos, Spain	31/10/2000 01/11/2000	3743812 3737858	00051720 00041607	10	1276 792	1.741 2.180	0.549
B6	Portman, Spain	01/11/2000	3735515	00041607	14	967	2.180	0.691 0.825
B7	Cartagena, Spain	01/11/2000	3735688	00049909	14	251	2.615	0.823
B8	La Azohia, Spain	02/11/2000	3733420	00109700	14	1643	2.885	0.826
B9	Mazarrón, Spain	02/11/2000	3733533	00115521	13	671	2.802	0.823
B10	Puntas del Calnegre, Spain	02/11/2000	3730667	00124518	7	238	2.305	0.772
B11	Cabo Cope, Spain	05/04/2001	3726366	00129107	11	1183	2.723	0.796
B12	Aguilas, Spain	05/04/2001	3723693	00136694	11	611	2.659	0.782
B13	San Juan de los Terreros, Spain	06/04/2001	3721767	00139730	13	1536	2.566	0.774
B14	Villaricos, Spain	06/04/2001	3715251	00146214	8	177	2.530	0.806
B15	Garrucha, Spain	06/04/2001	3712053	00149611	7	434	1.784	0.609
B16 B17	Playa de Macenas, Spain Punta de los Muertos, Spain	06/04/2001 08/12/2001	3704998 3657026	00151070 00154291	6	235 236	2.897 2.085	0.853 0.726
B17	Las Negras, Spain	08/12/2001		00200350	6	82	2.083	0.726
B19	El Pozo de los Frailes, Spain	22/04/2001		00203338	4	61	1.536	0.613
B20	Cabo de Gata, Spain	22/04/2001		00211410	5	42	1.750	0.654
B21	Retamar, Spain	29/10/2000		00218998	13	950	3.120	0.866
B22	Almeria, Spain	29/10/2000	3652422	00225276	12	480	2.219	0.734
B23	Roquetas de Mar, Spain	02/02/2002		00237258	9	984	2.493	0.788
B24	Punta del Sabinar, Spain	02/02/2002		00242711	11	1253	2.852	0.837
B25	Guardias Viejas, Spain	23/02/2002		00250991	7	1609	1.104	0.430
B26	Adra, Spain	23/02/2002 12/01/2002		00300657	13	389 385	2.647	0.764
B27 B28	La Rabita, Spain La Guapa, Spain	12/01/2002	3645008 3644587	00310820 00217628	9	315	2.132 2.138	0.733 0.678
B29	Calahonda, Spain	22/01/2000		00323886	12	936	2.733	0.814
B30	Torrenueva, Spain	22/12/2001		00329275	15	864	2.671	0.789
B31	Torrecuevas, Spain	21/04/2001		00341377	10	122	2.411	0.766
B32	Lagos, Spain	31/10/1999	3644608	00400418	12	973	2.263	0.702
B33	Torrex, Spain	31/10/1999	3644665	00355145	6	95	1.814	0.606
B34	Torre del Mar, Spain	05/05/2001		00407636	11	711	1.318	0.401
B35	Benajarafe, Spain	05/05/2001		00410774	9	376	2.222	0.702
B36	Benagalbon, Spain	20/05/2000		00414780	16 13	2255 484	2.662 3.079	0.787
B37	Malaga, Spain	20/05/2000 26/04/2000	3640961 3637862	00427297 00429801	18	583	2.837	0.861 0.810
B38 B39	Torremolinos, Spain Fuengirola, Spain	26/04/2000		00427801	19	940	2.881	0.810
B40	Los Jarales, Spain	16/12/2001	3629369	00443120	17	1096	1.805	0.562
B41	Marbella, Spain	21/04/2000	3630552	00451725	17	1661	2.799	0.809
B42	San Pedro de Alcantara, Spain	15/04/2000		00459776	15	381	2.680	0.781
B43	Rio del Padrón, Spain	20/11/1999		00506727	16	366	2.808	0.799
B44	Casares, Spain	20/11/1999		00513125	22	1105	3.026	0.814
B45	Cala Sardina, Spain	21/10/1999		00515564	13	660	2.564	0.790
B46	Sotogrande, Spain	29/01/2000		00517008	21	274	3.717	0.911
B47	La Línea, Spain	29/01/2000		00520402 00520871	8 15	1556 2067	1.600 1.484	0.580 0.536
B48 B49	Deadman's Beach, Gibraltar Getares, Spain	17/10/1999 12/04/2000		00525972	15	721	2.486	0.336
B50	Punta del Carnero, Spain	24/10/1999		00526307	11	268	2.824	0.843
B51	Punta del Cabrito, Spain	26/11/2000		00532400	11	318	1.880	0.597
B52	Rio Jara, Spain	27/11/1999		00537925	13	1295	1.700	0.520
B53	Punta Camarinal, Spain	27/11/1999	3605233	00547119	12	2786	2.357	0.779
B54	Zahara de los Atunes, Spain	04/12/1999		00551264	12	1131	2.168	0.644
B55	Barbate, Spain	12/04/2000		00554280	8	5332	2.051	0.703
B56	Cabo de Trafalgar, Spain	11/12/1999		00601888	8	3918	0.995	0.362
B57	Conil de la Frontera, Spain	12/02/2000		00606763	14	2059	1.985	0.609
B58	Codiz Spain	28/12/1999 14/04/2001		00609679 00615886	11	557 1919	2.671 1.515	0.790 0.476
B59 B60	Cadiz, Spain Rota, Spain	14/04/2001		00613886	13	2092	2.574	0.476
B61	Chipiona, Spain	13/05/2000		00625427	9	5241	1.348	0.504
B62	Sanlúcar de Barrameda, Spain	13/05/2000		00622228	11	5450	1.495	0.525
B63	Torre de la Higuera, Spain	25/11/2000		00633881	10	134	2.652	0.805
B64	Torre del Oro, Spain	25/11/2000	3705991	00643536	5	6	2.252	0.933
B65	Mazagon, Spain	26/01/2002		00647529	11	70	2.682	0.786

Appendix 1. The Biogeographical Sites

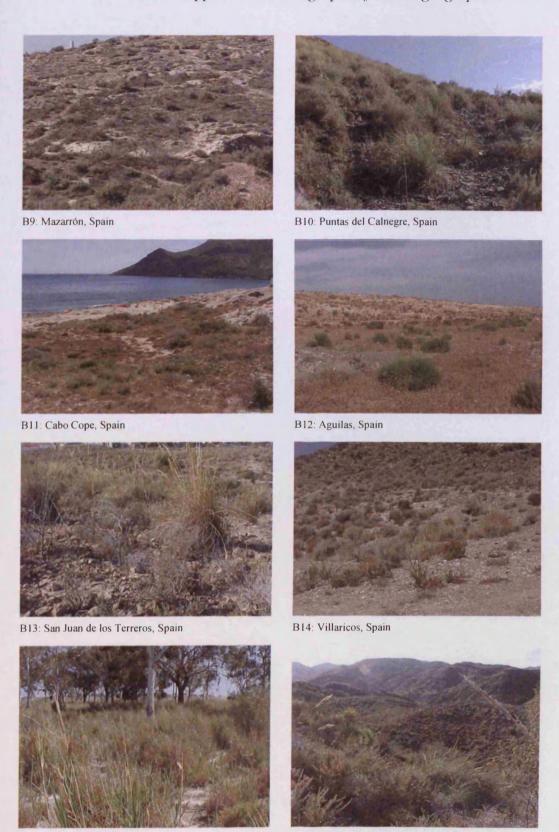
Site	Site Name	Date Sampled	Latitude	Longitude	No.	Total	Shannon	Simpson's
No.	Site Name	Date Sampleu	Latitude	Longitude	Spe	Abund	Diversity	Diversity
B66	Punta Umbria, Spain	26/01/2002	3711305	00658834	7	730	2.252	0.767
B67	El Rompido, Spain	26/05/2001	3713526	00708505	9	130	2.000	0.640
B68	Isla Cristina, Spain	26/05/2001	3711845	00718255	6	831	2.069	0.726
B69	Monte Gordo, Portugal	08/04/2000	3710698	00726633	5	800	1.826	0.672
B70	Tavira, Portugal	08/04/2000	3708297	00735683	15	1220	2.797	0.812
B71	Torre de Ares, Portugal	17/12/2000	3704475	00747749	19	1979	2.916	0.798
B72	Olhão, Portugal	17/12/2000	3704652	00751132	21	710	3.562	0.890
B73	, Faro, Portugal	16/12/2000	3701559	00756804	13	2452	2.495	0.761
B74	Vale do Lobo, Portugal	26/10/2000	3703695	00803584	16	383	2.869	0.818
B75	Albufeira, Portugal	26/10/2000	3705562	00815361	19	763	3.566	0.895
B76	Armação de Pera, Portugal	26/10/2000	3706486	00822933	17	1367	2.810	0.815
B77	Portimão, Portugal	25/10/2000	3709372	00835517	16	1203	2.239	0.688
B78	Luz, Portugal	25/10/2000	3705889	00843141	21	1284	3.495	0.875
B79	Burgau, Portugal	09/04/2000	3704632	00846742	16	609	2.827	0.790
B80	Salema, Portugal	25/10/2000	3704233	00849208	15	1624	3.062	0.829
B81	Cabo São Vicente, Portugal	09/04/2000	3701423	00859665	8	177	2.657	0.835
B82	Vila do Bispo, Portugal	24/10/2000	3705130	00857102	4	147	0.452	0.130
B83	Carrapateira, Portugal	24/10/2000	3710404	00854441	13	1282	0.836	0.219
B84	Praia da Carriagem, Portugal	24/10/2000	3721946	00850116	11	389	2.586	0.782
B85	Odeceixe, Portugal	23/10/2000	3726198	00848165	13	683	3.166	0.875
B86	Zambujeira do Mar, Portugal	23/10/2000	3731113	00847191	12	177	2.126	0.680
B87	Cabo Serdão Cavaleiro, Portugal	23/10/2000	3735014	00848734	4	11	1.981	0.818
B88	Milfontes, Portugal	22/10/2000	3743151	00846525	17	909	2.740	0.796
B89	Porto Covo, Portugal	22/10/2000	3750256	00847339	17_	2204	2.553	0.718
B90	Sines, Portugal	21/10/2000	3758183	00852025	13	614	2.620	0.768
B91	Lagoa de Santo André, Portugal	21/10/2000	3806556	00847502	16	1135	2.879	0.818



Appendix 2. Photographs of the Biogeographical Sites: B1 to B8. See Appendix 1 for site details.

B7: Cartagena, Spain

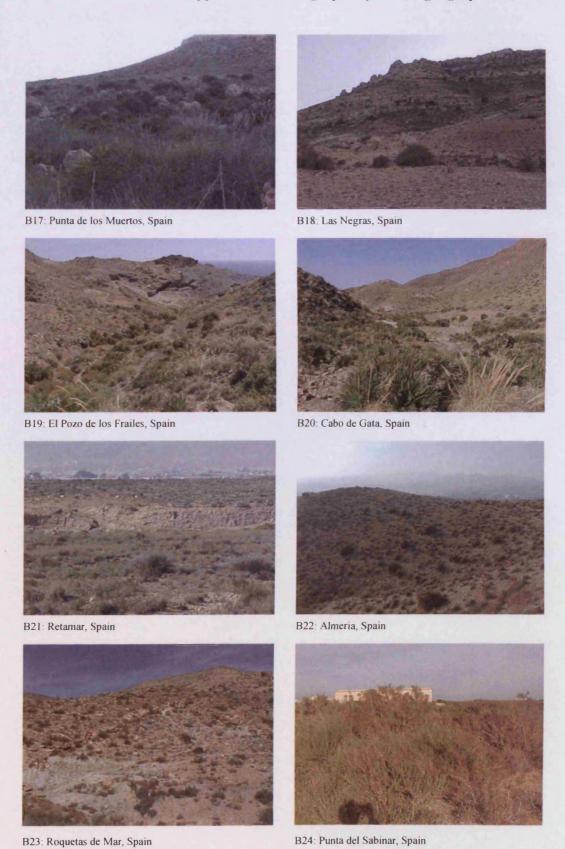
B8: La Azohia, Spain



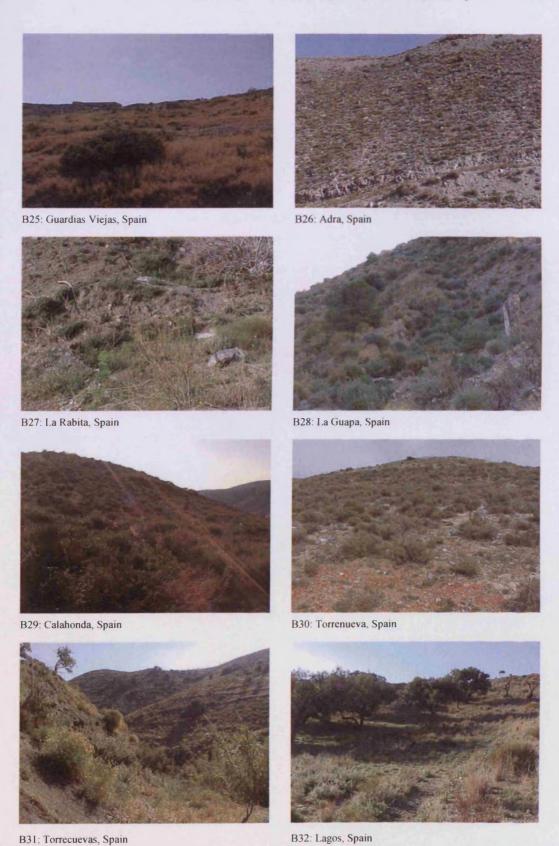
Appendix 2 (continued). Photographs of the Biogeographical Sites: B9 to B16. See Appendix 1 for site details.

B15: Garrucha, Spain

B16: Playa de Macenas, Spain



Appendix 2 (continued). Photographs of the Biogeographical Sites: B17 to B24. See Appendix 1 for site details.



Appendix 2 (continued). Photographs of the Biogeographical Sites: B25 to B32. See Appendix 1 for site details.

Appendix 2. Photographs of the Biogeographical Sites



Appendix 2 (continued). Photographs of the Biogeographical Sites: B33 to B40. See Appendix 1 for site details.

B40: Los Jarales, Spain

B39: Fuengirola, Spain



Appendix 2 (continued). Photographs of the Biogeographical Sites: B41 to B48. See Appendix 1 for site details.



Appendix 2 (continued). Photographs of the Biogeographical Sites: B49 to B56. See Appendix 1 for site details.

B55: Barbate, Spain

B56: Cabo de Trafalgar, Spain



B57: Conil de la Frontera, Spain



B58: Chiclana de la Frontera, Spain



B59: Cadiz, Spain



B60: Rota, Spain



B61: Chipiona, Spain



B62: Sanlúcar de Barrameda, Spain

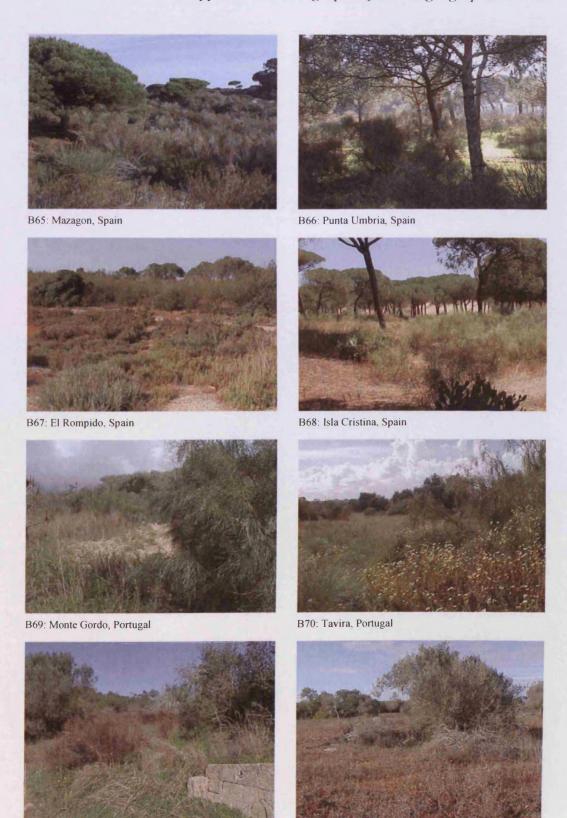


B63: Torre de la Higuera, Spain



B64: Torre del Oro, Spain

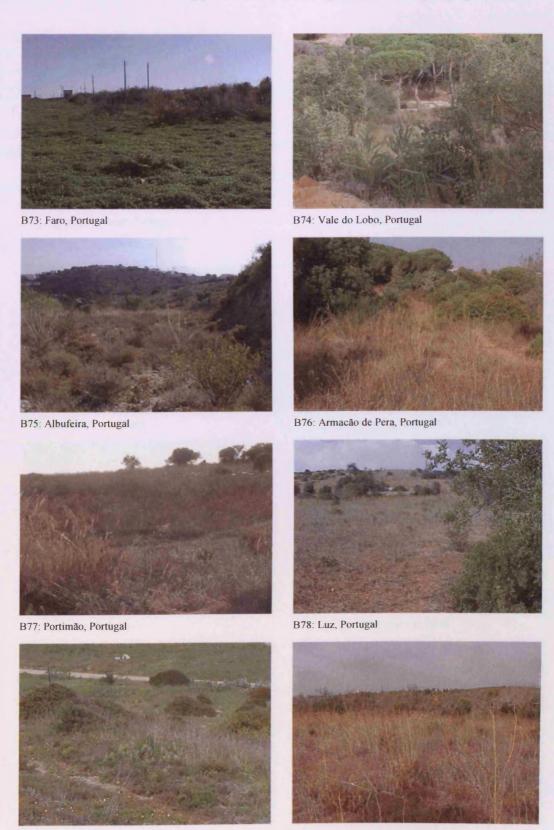
Appendix 2 (continued). Photographs of the Biogeographical Sites: B57 to B64. See Appendix 1 for site details.



Appendix 2 (continued). Photographs of the Biogeographical Sites: B65 to B72. See Appendix 1 for site details.

B71: Torre de Ares, Portugal

B72: Olhão, Portugal

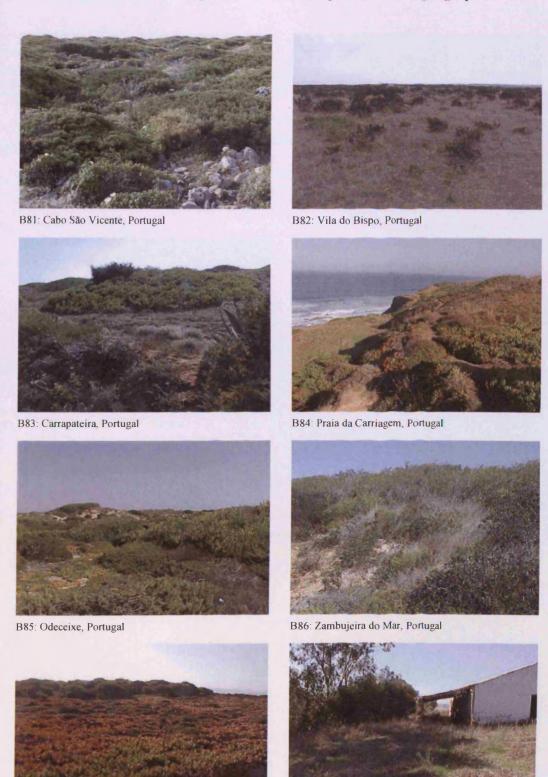


Appendix 2 (continued). Photographs of the Biogeographical Sites: B73 to B80. See Appendix 1 for site details.

B79: Burgau, Portugal

B80: Salema, Portugal

Appendix 2. Photographs of the Biogeographical Sites



B87: Cabo Serdão Cavaleiro, Portugal

Appendix 2 (continued). Photographs of the Biogeographical Sites: B81 to B88. See Appendix 1 for site details.

B88: Milfontes, Portugal

Appendix 2. Photographs of the Biogeographical Sites



B89: Porto Covo, Portugal



B90: Sines, Portugal



B91: Lagoa de Santo André, Portugal

Appendix 2 (continued). Photographs of the Biogeographical Sites: B89 toB 91. See Appendix 1 for site details.

Appendix 3. Systematic list of species including the sites at which each species was present. Biogeographical Sites (Part One) are prefixed with 'B' and Habitat Structure Sites (Part Two) are prefixed with 'S'. Data for number of sites, range, and rank are for Biogeographical Sites only. Systematic listing follows Falkner *et al.* (2002); the genus *Iberus* is treated here as polytypic (see Lopez-Alcantara *et al.*, 1985; Puente, 1994; Arrébola, 1995; Elejalde *et al.*, 2005, and Gallego, 2006 for discussions on the generic status of *Iberus*). See Appendix 1 and Table 6.1 for site names.

Family and species	No. of sites	Range	Rank	
ACICULIDAE				
Acicula norrisi Gittenberger & Boeters, 1977	B48	1	М	75
POMATHDAE				
Leonia mamillaris (Lamarck, 1822)	B1, B2, B5-11, B13	10	М	19
CARYCHIIDAE				-
Carychium minimum Müller, 1774	B78	1	A	61
			7.5	-
COCHLICOPIDAE				
Hypnophila malagana Gittenberger & Menkhorst, 1983	B2, B28, B31	3	М	71
PUPILLIDAE				
	B62, B71, B72, B77, B78, B83, B85,	1.0		
Lauria (Lauria) cylindracea (Da Costa, 1778)	B88, B89, B91	10	A	16
VALLONIIDAE		-	4	
Vallonia costata (Müller, 1774)	B38, B60, B62	3	MA	42
Vallonia excentrica Sterki, 1892	B71	- 1	A	66
Vallonia pulchella (Müller, 1774)	B78	1	A	58
		761-4		
PYRAMIDULIDAE				
Pyramidula pusilla (Vallot, 1801)	B34, B38, B40, B41, B46, B63, B65, B68, B70, B71, B74, B78, B83, B85, B86, B88, B89, B90, B91	19	MA	15
CHONDRINIDAE				
CHONDRINIDAE	B1-3, B5, B6, B8-14, B16, B21-23,			
Granopupa granum (Draparnaud, 1801)	B26, B29, B30, B32, B44, B53, B72,	25	MA	10
	B75, B76, S2, S33, S36, S49			
Chondrina calpica calpica (Westerlund, 1872)	S33			
VERTIGINIDAE				
Truncatellina callicratis (Scacchi, 1833)	B72	- 1	A	57
Truncatellina claustralis (Gredler, 1856)	B78	1	A	68
Truncatellina cylindrica (Férussac, 1807)	B1, B2, B6, B8, B13, B14, B16, B20, B24, B29, B34, B39-41, B43, B44, B46, B54, B56, B57, B60, B61, B71, B72, B75, B76, B79, B80, B83-85, B87-91	35	MA	6
FERUSSACIIDAE				
Cecilioides (Cecilioides) jani (De Betta & Martinati, 1855)	B6, B8, B22, B29, B30, B32, B34, B38, B39, B43, B44, B46, B48, B49, B53, B54, B57, B58, B70-77, B79, B83	28	MA	35
Cecilioides (Cecilioides) acicula (Müller, 1774)	B2, B6, B8, B14, B20, B21, B27, B30, B36, B61, B62, B70, B72, B75, B78, B80, S31	16	MA	37
Ferussacia (Ferussacia) folliculus (Gmelin, 1790)	B1-17, B19, B21, B22, B27-50, B52, B53, B54, B55, B57, B58, B64-67, B70-80, B83, B90, B91, S2, S21, S23-26, S30, S31, S33, S36, S41, S43, S44, S49, S52, S53, S56, S57, S60	68	MA	3
Johenwartiana eucharista (Bourguignat, 1864)	B23, B26, B28	3	М	29

Family and species	Sites at which present	No. of sites	of Range		
SUBULINIDAE					
Rumina decollata (Linnaeus, 1758)	B1-14, B16-18, B21-23, B26-33, B35, B37, B38, B40-44, B46, B48, B49, B56, B57, B59, B60, B63, B67, B71, B73-76, B78, B80, B81, B84, B87-90, S2, S21, S31, S34-36, S58, S59				
THOMAS OF LAND	Committee of the second				
TESTACELLIDAE Testacella maugei Férussac, 1819	B38, B39, B42, B46, B49, B50, B57, B79, S44	8	MA	67	
DUNCTIDAE					
PUNCTIDAE Punctum (Punctum) pygmaeum (Draparnaud, 1801)	B51, B72, B76, B86	4	A	53	
Paralaoma caputspinulae (Reeve, 1852)	B75, B77, B79, B88	4	A	63	
PRISTILOMATIDAE					
Vitrea (Vitrea) contracta (Westerlund, 1871)	B6, B40, B44, B72, B74-80, B83-86, B88, B89	17	MA	28	
EUCONULIDAE					
Euconulus (Euconulus) fulvus (Müller, 1774)	B89	1	A	75	
BULIMINIDAE					
Mastus pupa (Linnaeus, 1758)	B57, S53	1	A	74	
OXYCHILIDAE					
Oxychilus (Oxychilus) cellarius (Müller, 1774)	B40	1	М	73	
Oxychilus (Oxychilus) draparnaudi (Beck, 1837)	B37-42, B44, B46, B48, B49, B53, B75, B78, B90, B91, S22, S25, S33, S35, S41, S44, S48	15	MA	36	
Oxychilus (Oxychilus) hydatīnus (Rossmässler, 1854)	B3, B39, B53, S33	3	MA	70	
Oxychilus spl	B6	1	М	70	
Oxychilus sp2	B77	1	A	74	
Oxychilus sp3	B6, B31	2	M	74	
PARMACELLIDAE		F - 1			
Parmacella (Parmacella) valencieni Webb & van Beneden, 1836	B30, B36, B39, B42, B43, B48-50, B65, B74-76, B80, B88, S29	14	МА	54	
MILACIDAE					
Milax gagates (Draparnaud, 1801)	B3, B28, B30, B32, B39, B40, B42, B44, B45, B71, B72, S2, S25, S26, S42-44, S47	11	MA	51	
Milax nigricans (Schluz, 1836)	B4, B40, B44, B46, B50, B51, B54, B72, B91, S22, S23, S28	9	MA	49	
				24 2	
LIMACIDAE Limax (Limacus) flavus Linnaeus, 1758	B70, B88	2	A	72	
Lehmania valentiana (Férussac, 1821)	B3, B26, B30, B35, B38-42, B62, B73, B91	12	MA	46	
ACDIOLIMACIDAE	3				
AGRIOLIMACIDAE Deroceras (Deroceras) panormitanum (Lessona & Polonera, 1882)	B38	1	М	59	
Deroceras (Agriolimax) reticulatum (Müller, 1774)	B38	1	М	75	
Deroceras (Agriolimax) nitidum (Morelet, 1845)	B86	1	A	72	
Deroceras (Agriolimax) ponsonbyi (Hesse, 1884)	B46, B51	2	MA	69	
Deroceras sp	S43			4	

Family and species	Family and species Sites at which present				
SPHINCTEROCHILIDAE		sites			
Sphincterochila (Albea) candidissima (Draparnaud, 1801)	B13, B17, B21	3	М	38	
Spnincterochila (Cariosula) baetica (Rossmässler, 1854)	B1, B7-9, B12, B22-24	8	М	25	
ARIONIDAE					
Geomalacus malagensis Wiktor & Norris, 1991	omalacus malagensis Wiktor & Norris, 1991 B40, B43, B46, B48, B49, B51, S2, S22, S25, S26, S30, S42		MA	61	
TRISSEXODONTIDAE					
Caracollina (Caracollina) lenticula (Michaud, 1831)	B1-18, B21-32, B34-37, B39-48, B52-55, B58-61, B63, B65-67, B70, B71, B73-80, B83, B85, B86, B88- 91, S2, S9, S30-35, S41, S42, S44, S49, S52, S53, S55, S56, S59	73	MA	4	
Gasulliella simplicula (Morelet, 1845)	B43-45, B49, B52, B54, S32, S44	6	MA	44	
Gittenbergeria turriplana (Morelet, 1845)	B71, B72, B75, B76, S58	4	A	20	
Oestophora barbula (Rossmässler, 1838)	B84, B86, B88, B89, S46	4	A	52	
Oestophora calpeana (Morelet, 1854)	B48, S25, S33, S35, S52	1	M	73	
Oestophora tarnieri (Morelet, 1854)	B51, S43	1	A	74	
Oestophora ortizi de Winter and Ripken, 1991	S21				
Oestophora sp1 Oestophora sp2	B82	1	A	71	
Hatumia pseudogasulli Arrébola, Prieto, Puente and Ruiz, 2006	B19, B20, B27, B31, B33	- 5	М	60	
HYGROMIIDAE					
Cochlicella (Cochlicella) acuta (Müller, 1774)	B2-5, B7, B11-13, B15, B24-26, B30, B34-39, B41, B46-48, B52-63, B68, B70-73, B75-78, B80, B83, B85, B88, B89, B91, S1-6, S8, S10, S11, S14-18, S30, S34, S36, S38, S40, S41, S49, S53, S55	50	MA	2	
Cochlicella (Cochlicella) conoidea (Draparnaud, 1801)	B24, B34, B41, B47, B52-56, B58, B59, B62, B68, B70, B81, B83, S1, S3-7, S11, S13, S16, S18, S41, S51, S55	16	MA	12	
Cochlicella (Prietocella) barbara (Linnaeus, 1758)	B3, B7, B21, B29, B36-38, B41-47, B60-62, B65, B67, B69-74, B77, B78, B84, B85, B88, B89, B91, S28, S43, S53	32	МА	13	
Trochoidea (Trochoidea) elegans (Gmelin, 1791)	B5, B32, B36	3	М	32	
Trochoidea (Trochoidea) pyradimata (Draparnaud, 1805)	B2, B12, S17	2	М	22	
Trochoidea (Xerocrassa) barceloi (Hidalgo, 1878)	B2	1	М	75	
Trochoidea (Xerocrassa) derogata (Rossmässler, 1854)	B1, B8, B10, B13, B14, B16, B23, B26, S20	8	М	21	
Trochoidea (Xerocrassa) murcica (Guirao in Rossmässler, 1854)	B11, B13, B16, B21, B24-26, B28	8	М	27	
Trochoidea (Xerocrassa) jimenensis Puente & Arrébola, 1996	B44, B45, B60	3	MA	67	
Trochoidea sp1	B56, S33	1	A	48	
Trochoidea sp2	B67, B74, B87, S35, S52	3	A	72	
Trochoidea sp3	B64, \$53	1	A	75	
Trochoidea sp4	S55, S56		100		
Trochoidea sp5	S43				
Trochoidea sp6	S24				
Trochoidea sp7 Ponentina subvirescens (Bellamy, 1839)	\$36, \$57, \$58 \$63-67, \$74, \$82, \$86, \$90, \$91, \$2, \$31, \$41, \$42-47, \$49, \$50, \$54, \$55, \$57, \$60	10	A	47	

Family and species	Family and species Sites at which present					
Trichia martigena (Férussac, 1821)	B45	sites	M	64		
Xerotrichia conspurcata (Draparnaud, 1801)	B16, B18, B19, B20, B27, B28, B31, B33, B34, B36-47, B52, B54, B55, B57, B59, B60, B61, B63, B65, B66, B71, B73-75, B77-79, B81, B86, S2, S9, S14, S21, S24, S25, S30, S37, S41, S43, S44, S53, S54, S55, S59, S60	40	MA	8		
Xerotrichia apicina (Lamarck, 1822)	B36-41, B45-49, B52-55, B57-62, B68-71, B73, B74, B76, B77, B79, B89, S1-14, S16, S17, S18, S22, S27, S28, S30, S37, S41, S43, S51	31	MA	5		
Xeroleuca vatonniana (Bourguignat, 1867)	B78, B84, B85	3	A	50		
Helicella huidobroi (Azpeitia, 1925)	B1, B2, B7	3	M	47		
Helicella? stiparum (Rossmässler, 1854)	B21, B22, B24, B25, S20	4	М	23		
Candidula gigaxii (Pfeiffer, 1848)	B39, B44, B79	3	MA	60		
Candidula intersecta (Poiret, 1801) Candidula sp1	B82, S21, S25, S28, S29 B81, B86, B90, S45	3	A	74 55		
Candidula sp2	B81, B86, B90, S45 B72, B89, S36	2	A	62		
Candidula sp3	S20		/1	02		
Cernuella (Cernuella) virgata (Da Costa, 1778)	B9, B37, B41, B44-46, B49-52, B58, B80, S22, S27, S28, S32, S37, S41, S45, S46	12	MA	26		
Xerosecta (Xerosecta) adolfi (Pfeiffer, 1854)	B24	1	М	50		
Xerosecta (Xerosecta) cespitum (Draparnaud, 1801)	B32, B35, B36, B43, B44, B49-51, B57, B72, B77-80, S24, S41, S44, S49, S55, S56	14	MA	34		
Xerosecta (Xerosecta) promissa (Westerlund, 1893)	B1, B3-5, B7, B9, B15, B22, B26, B32, B36-39, B41-46, B49, B50, B52, B56, B58, B64, B70-73, B75- 80, S10-12, S14, S22, S27, S32, S34, S38-40, S49	36	MA	11		
Xerosecta (Xerosecta) reboudiana (Bourguignat, 1863)	B29, B31-36, B39, S17, S26, S31, S53, S57	8	М	24		
Xerosecta sp	B79	1	A	56		
Portugala inchoata (Morelet, 1845)	B67, B81-91	12	A	31		
Microxeromagna armillata (Lowe, 1852)	B3, B6, B11, B12, B15, B17, B24, B26, B29, B30, B41, B53, B57, B63, B65-72, B74-76, B78, B80, B83, B84, B85, B88-91	34	MA	9		
Ganula gadirana Muñoz, Almodovar & Arrébola, 1999	B51, B52, S22	2	Α	74		
Iberus gualtierianus marmoratus (Férussac, 1821)	B6-9, B31, B48, S2, S9, S24, S30, S33, S43, S46, S48, S52	6	М	39		
Iberus gualtierianus alonensis (Férussac, 1821)	B1-3, B8, B9, B11-14, B16, B19-23, B26, B27, B29, B33, B63, S31	20	MA	33		
Iberus gualtierianus gualtieranus (Linnaeus, 1758)	B22, B23	2	M	43		
Iberus gualtierianus globulosus Boettger, 1913	B17, B18, B25, B26, B30, B31	6	М	41		
Theba pisana (Müller, 1774)	B1-5, B7-9, B11-13, B15, B18, B21, B22, B25, B29, B30, B32, B34-63, B65-81, B83-85, B88-91, S1-18, S22, S28, S30, S32, S34, S36-39, S41, S45, S48, S49, S51-53, S55, S56, S58-60	73	MA	1		
Theba gittenbergeri Puente, 1994	B24, S58	1	М	40		
Theba subdentata helicella (Wood, 1828) B21		1	M	65		
Pseudotachea litturata (Pfeiffer, 1851)	B1, B6, B43, B44, B46, B50, S42, S43, S45 B8-13, B15, B16, B18, B22, B29,	6	MA	45		
Otala (Otala) lactea (Müller, 1774)	60	МА	7			
	S32, S33, S35, S36, S41-43, S45, S48, S49, S52-58 B1-3, B7, B21, B23-28, B30, B36,					

Family and species	Sites at which present	No. of sites	Range	Rank
Eobania vermiculata (Müller, 1774)	B1-5, B7, B9, B40, B42, B59, B60, S7, S16, S34	11	MA	30
Cantareus aspersus (Müller, 1774)	B7, B30, B36-44, B46, B48-52, B57-63, B65, B70-81, B84-86, B88-91, S2, S8, S9, S14, S16, S22, S23, S25, S28-30, S32, S34, S35, S37, S39, S41, S43-45, S47, S48, S50, S52, S53, S56, S58-60	44	MA	17

Appendix 4. The species and their abundances at the Biogeographical Sites. See Appendix 1 for site numbering and details, and Appendix 3 for species' authors.

Species	B1	B2	В3	B4	B5	B6	B7
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	315	-1	0	0	5	17	3
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	2	0	0	0	0	0
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	0	0	0	0	0
Granopupa granum	481	134	1	0	1	298	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	3	1	0	0	0	35	0
Cecilioides (Cecilioides) jani	0	0	0	0	0	14	0
Cecilioides (Cecilioides) acicula	0	2	0	0	0	11	0
Ferussacia (Ferussacia) folliculus	68	80	46	89	73	105	10
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	5	113	84	3	7	50	11
Testacella maugei	0	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	0	10	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	2	0	0	0	0
Oxychilus sp1	0	0	0	0	0	7	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	1	0
Parmacella (Parmacella) valencieni	0	0	0	0	0	0	0
Milax gagates	0	0	1	0	0	0	0
Milax nigricans	0	0	0	3	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	1	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	6	0	0	0	0	0	1
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	34	278	72	130	22	155	40
Gasulliella simplicula	0	0	0	0	0	0	0
Gusumena simplicula Gittenbergeria turriplana	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	0
Oestophora varvuta Oestophora calpeana	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
Oestophora tarnieri	0	0	0	0	0	0	0
Oestophora spl	0	0	0	0	0	0	0
Hatumia pseudogasulli Cochlicella (Cochlicella) acuta	0	719	399	65	142	0	20

Appendix 4 (continued). Species	B1	B2	B3	B4	B5	B6	B7
Cochlicella (Cochlicella) conoidea	0	0	0	0	0	0	0
Cochlicella (Prietocella) barbara	0	0	39	0	0	0	3
Trochoidea (Trochoidea) elegans	0	0	0	0	6	0	0
Trochoidea (Trochoidea) pyradimata	0	485	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	1	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	207	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	0	0	0	0	0	0	0
Xerotrichia apicina	0	0	0	0	0	0	0
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	76	6	0	0	0	0	1
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	0	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	2	0	132	107	91	0	113
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	0	0	1	0	0	159	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	103	5
Iberus gualtierianus alonensis	56	13	4	0	0	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	65	250	1350	832	397	0	16
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	44	0	0	0	0	2	0
Otala (Otala) lactea	0	0	0	0	0	0	0
Otala (Otala) punctata	41	58	20	0	0	0	2
Eobania vermiculata	70	38	37	47	48	0	25
Cantareus aspersus	0	0	0	0	0	0	1

Appendix 4 (continued).										
Species	B8	B9	B10	B11	B12	B13	B14			
Acicula norrisi	0	0	0	0	0	0	0			
Leonia mamillaris	441	6	53	29	0	1	0			
Carychium minimum	0	0	0	0	0	0	0			
Hypnophila malagana	0	0	0	0	0	0	0			
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0			
Vallonia costata	0	0	0	0	0	0	0			
Vallonia excentrica	0	0	0	0	0	0	0			
Vallonia pulchella	0	0	0	0	0	0	0			
Pyramidula pusilla	0	0	0	0	0	0	0			
Granopupa granum	425	23	71	57	80	619	8			
Truncatellina callicratis	0	0	0	0	0	0	0			
Truncatellina claustralis	0	0	0	0	0	0	0			
Truncatellina cylindrica	15	0	0	0	0	21	2			
Cecilioides (Cecilioides) jani	13	0	0	0	0	0	0			
Cecilioides (Cecilioides) acicula	8	0	0	0	0	0	4			
Ferussacia (Ferussacia) folliculus	44	35	16	7	18	191	40			
Hohenwartiana eucharista	0	0	0	0	0	0	0			
Rumina decollata	133	175	10	122	5	67	24			
Testacella maugei	0	0	0	0	0	0	0			
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0			
Paralaoma caputspinulae	0	0	0	0	0	0	0			
Vitrea (Crystallus) contracta	0	0	0	0	0	0	0			
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0			
Mastus pupa	0	0	0	0	0	0	0			
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0			
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	0	0			
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0			
Oxychilus spl	0	0	0	0	0	0	0			
Oxychilus sp2	0	0	0	0	0	0	0			
Oxychilus sp3	0	0	0	0	0	0	0			
Parmacella (Parmacella) valencieni	0	0	0	0	0	0	0			
Milax gagates	0	0	0	0	0	0	0			
Milax nigricans	0	0	0	0	0	0	0			
Limax (Limacus) flavus	0	0	0	0	0	0	0			
Lehmania valentiana	0	0	0	0	0	0	0			
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0			
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0			
Deroceras (Agriolimax) reticularium Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0			
Deroceras (Agriolimax) minaum Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0			
Sphincterochila (Albea) candidissima	0	0	0	0	0	173	0			
Sphnincterochila (Cariosula) baetica	173	2	0	0	23	0	0			
Geomalacus malagensis	0	0	0	0	0	0	0			
Caracollina (Caracollina) lenticula	78	47	20	129	30	81	40			
	0	0	0	0	0	0	0			
Gasulliella simplicula	0	0	0	0	0	0	0			
Gittenbergeria turriplana Oastonborg barbula	0	0	0	0	0	0	0			
Oestophora galnagra	0	0	0	0	0	0	0			
Oestophora calpeana	0	0	0	0	0	0	0			
Oestophora tarnieri	0	0	0	0	0	0	0			
Oestophora sp1	0	0	0	0	0	0	0			
Hatumia pseudogasulli Cochlicella (Cochlicella) acuta	0	0	0	439	9	1	0			

Appendix 4 (continued).							
Species	B8	B9	B10	B11	B12	B13	B14
Cochlicella (Cochlicella) conoidea	0	0	0	0	0	0	0
Cochlicella (Prietocella) barbara	0	0	0	0	0	0	0
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	70	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	162	0	67	0	0	3	47
Trochoidea (Xerocrassa) murcica	0	0	0	46	0	240	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	0	0	0	0	0	0	0
Xerotrichia apicina	0	0	0	0	0	0	0
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	5	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	0	131	0	0	0	0	0
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	0	0	0	15	73	0	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	120	2	0	0	0	0	0
Iberus gualtierianus alonensis	8	1	0	17	1	6	12
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	1	157	0	202	57	4	0
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	22	48	1	120	245	129	0
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	39	0	0	0	0	0
Cantareus aspersus	0	0	0	0	0	0	0

Appendix 4 (continued). Species	B15	B16	B17	B18	B19	B20	B21
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	0	0	0	0	0
Granopupa granum	0	3	0	0	0	0	150
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	0	24	0	0	0	1	0
Cecilioides (Cecilioides) jani	0	0	0	0	0	0	0
Cecilioides (Cecilioides) acicula	0	0	0	0	0	7	40
Ferussacia (Ferussacia) folliculus	4	45	53	0	2	0	123
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	0	5	15	13	0	0	97
Testacella maugei	0	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	0	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	0	0	0	0	0	0	0
Milax gagates	0	0	0	0	0	0	0
Milax nigricans	0	0	0	0	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	0	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ritidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	1	0	0	0	77
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	26	55	29	16	0	0	181
Gasulliella simplicula	0	0	0	0	0	0	0
Gasumena simpucuta Gittenbergeria turriplana	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	0
Oestophora calpeana	0	0	0	0	0	0	
Oestophora tarnieri	0	0	0	0	0	0	0
Oestophora spl	0	0	0	0	7	2	0
Hatumia pseudogasulli Cochlicella (Cochlicella) acuta	29	0	0	0	0	0	$\frac{0}{0}$

Appendix 4 (continued). Species	B15	B16	B17	B18	B19	B20	B21
Cochlicella (Cochlicella) conoidea	0	0	0	0	0	0	0
Cochlicella (Prietocella) barbara	0	0	0	0	0	0	1
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	31	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	28	0	0	0	0	45
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	0	20	0	8	20	22	0
Xerotrichia apicina	0	0	0	0	0	0	0
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	26
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	0	0	0	- 0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	4	0	0	0	0	0	0
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	19	0	101	0	0	0	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	0	0
Iberus gualtierianus alonensis	0	23	0	0	32	10	9
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	37	40	0	0	0
Theba pisana	247	0	0	4	0	0	12
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	13
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	105	1	0	1	0	0	0
Otala (Otala) punctata	0	0	0	0	0	0	176
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	0	0	0	0	0	0	0

Appendix 4 (continued). Species	B22	B23	B24	B25	B26	B27	B28
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	2
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	0	0	0	0	0
Granopupa granum	2	1	0	0	13	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	0	0	333	0	0	0	0
Cecilioides (Cecilioides) jani	1	0	0	0	0	0	0
Cecilioides (Cecilioides) acicula	0	0	0	0	0	3	0
Ferussacia (Ferussacia) folliculus	1	0	0	0	0	152	32
Hohenwartiana eucharista	0	343	0	0	4	0	6
Rumina decollata	19	14	0	0	45	48	6
Testacella maugei	0	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	0	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	0	0	0	0	0	0	0
Milax gagates	0	0	0	0	0	0	21
Milax nigricans	0	0	0	0	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	0	0	64	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	200	94	1	0	0	0	0
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	95	197	127	19	31	90	165
Gasulliella simplicula	0	0	0	0	0	0	0
Gittenbergeria turriplana	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	0
Oestophora calpeana	0	0	0	0	0	0	0
Destophora tarnieri	0	0	0	0	0	0	0
Destophora sp1	0	0	0	0	0	0	0
Hatumia pseudogasulli	0	0	0	0	0	6	0
Cochlicella (Cochlicella) acuta	0	0	238	46	5	0	0

Species	B22	B23	B24	B25	B26	B27	B28
Cochlicella (Cochlicella) conoidea	0	0	38	0	0	0	0
Cochlicella (Prietocella) barbara	0	0	0	0	0	0	0
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	49	0	0	19.	0	0
Trochoidea (Xerocrassa) murcica	0	0	4	1	24	0	46
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	0	0	0	0	0	5	1
Xerotrichia apicina	0	0	0	0	0	0	0
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	93	0	50	384	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	0	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	78	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	2	0	0	0	2	0	0
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	0	0	164	0	1	0	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	0	0
Iberus gualtierianus alonensis	1	10	0	0	3	2	0
Iberus gualtierianus gualtierianus	2	131	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	1	12	0	0
Theba pisana	4	0	0	1152	0	0	0
Theba gittenbergeri	0	0	187	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	60	0	0	0	0	0	0
Otala (Otala) punctata	0	145	33	6	166	79	36
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	0	0	0	0	0	0	0

Appendix 4 (continued). Species	B29	B30	B31	B32	B33	B34	B35
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	2	0	0	0	0
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	0	0	0	1	0
Granopupa granum	30	7	0	45	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	70	0	0	0	0	5	0
Cecilioides (Cecilioides) jani	4	8	0	42	0	2	0
Cecilioides (Cecilioides) acicula	0	9	0	0	0	0	0
Ferussacia (Ferussacia) folliculus	232	99	16	461	57	41	183
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	2	12	3	2	7	0	1
Testacella maugei	0	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	0	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus spl	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	1	0	0	0	0
Parmacella (Parmacella) valencieni	0	8	0	0	0	0	0
Milax gagates	0	5	0	2	0	0	0
Milax nigricans	0	0	0	0	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	2	0	0	0	0	14
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	279	289	15	237	0	2	33
Gasulliella simplicula	0	0	0	0	0	0	0
Gittenbergeria turriplana	0	0	0	0	0	0	0
Destophora barbula	0	0	0	0	0	0	0
Destophora calpeana	0	0	0	0	0	0	0
Destophora tarnieri	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
Oestophora sp1	0	0	3	0	5	0	0
Hatumia pseudogasulli Cochlicella (Cochlicella) acuta	0	22	0	0	0	3	12

Appendix 4 (continued). Species	B29	B30	B31	B32	B33	B34	B35
Cochlicella (Cochlicella) conoidea	0	0	0	0	0	5	0
Cochlicella (Prietocella) barbara	1	0	0	0	0	0	0
Trochoidea (Trochoidea) elegans	0	0	0	10	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	0	0	1	0	12	42	0
Xerotrichia apicina	0	0	0	0	0	0	0
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	0	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	0	0	56	0	0	4
Xerosecta (Xerosecta) promissa	0	0	0	3	0	0	0
Xerosecta (Xerosecta) reboudiana	79	0	42	77	2	62	75
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	54	25	0	0	0	0	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	3	0	0	0	0
Iberus gualtierianus alonensis	83	0	0	0	12	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	18	36	0	0	0	0
Theba pisana	2	182	0	3	0	544	13
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	100	0	0	35	0	4	41
Otala (Otala) punctata	0	172	0	0	0	0	0
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	0	6	0	0	0	0	0

Appendix 4 (continued). Species	B36	B37	B38	B39	B40	D41	D.43
Acicula norrisi	0	0	0	0		B41	B42
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0		-	0	0
	0	0	_	0	0	0	0
Hypnophila malagana	0	_	0	0	0	0	0
Lauria (Lauria) cylindracea Vallonia costata	0	0	124	0	0	0	0
Vallonia excentrica	0	0	134	0	0	0	0
			0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	32	0	673	5	0
Granopupa granum	0	0	0	0	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	0	0	0	105	6	8	0
Cecilioides (Cecilioides) jani	0	0	2	1	0	0	0
Cecilioides (Cecilioides) acicula	4	0	0	0	0	0	0
Ferussacia (Ferussacia) folliculus	22	45	1	6	9	3	6
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	0	2	3	0	14	24	11
Testacella maugei	0	0	1	2	0	0	1
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	10	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	3	0	0
Oxychilus (Oxychilus) draparnaudi	0	1	154	12	5	15	1
Oxychilus (Oxychilus) hydatinus	0	0	0	4	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	1	0	0	4	0	0	1
Milax gagates	0	0	0	4	12	0	1
Milax nigricans	0	0	0	0	7	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	2	3	3	3	6
Deroceras (Deroceras) panormitanum	0	0	24	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	1	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	0	0	0	2	0	0
Caracollina (Caracollina) lenticula	94	24	0	143	265	62	137
Gasulliella simplicula	0	0	0	0	0	0	0
Gittenbergeria turriplana	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	0
Oestophora calpeana	0	0	0	0	0	0	0
Oestophora tarnieri	0	0	0	0	0	0	0
Oestophora sp1	0	0	0	0	0	0	0
Hatumia pseudogasulli	0	0	0	0	0	0	0
Cochlicella (Cochlicella) acuta	602	102	5	30	0	393	0

Species	B36	B37	B38	B39	B40	B41	B42
Cochlicella (Cochlicella) conoidea	0	0	0	0	0	51	0
Cochlicella (Prietocella) barbara	2	13	20	0	0	4	6
Trochoidea (Trochoidea) elegans	292	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	751	26	142	352	13	130	25
Xerotrichia apicina	6	93	1	17	11	476	0
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	4	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	2	0	0	0	3	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	14	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	143	12	12	1	0	25	39
Xerosecta (Xerosecta) reboudiana	195	0	0	19	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	0	0	0	0	0	102	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	0	0
Iberus gualtierianus alonensis	0	0	0	0	0	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	63	43	20	51	3	334	_ 26
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	26	0	9	86	0	0	18
Otala (Otala) punctata	35	84	0	0	0	0	0
Eobania vermiculata	0	0	0	0	6	0	3
Cantareus aspersus	5	37	20	96	54	23	100

Appendix 4 (continued). Species	B43	B44	D45	DAC	DAT	D.40	D 40
			B45	B46	B47	B48	B49
Acicula norrisi	0	0	0	0	0	1	0
Leonia mamillaris Carychium minimum	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	0	13	0	0	0
Granopupa granum	0	13	0	0	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	1	1	0	6	0	0	0
Cecilioides (Cecilioides) jani	4	30	0	1	0	14	1
Cecilioides (Cecilioides) acicula	0	0	0	0	0	0	0
Ferussacia (Ferussacia) folliculus	84	20	107	35	207	1241	255
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	5	21	0	1	0	23	5
Testacella maugei	0	0	0	1	0	0	2
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	1	0	0	0	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	8	0	1	0	11	1
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	5	0	0	0	0	2	6
Milax gagates	0	2	2	0	0	0	0
Milax nigricans	0	2	0	4	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	0	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	5	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	4	0	0	1	0	10	4
Caracollina (Caracollina) lenticula	122	127	205	27	33	28	0
Gasulliella simplicula	1	48	12	0	0	0	1
Gittenbergeria turriplana	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	0
Oestophora calpeana	0	0	0	0	0	3	0
Destophora tarnieri	0	0	0	0	0	0	0
Oestophora sp1	0	0	0	0	0	0	0
Hatumia pseudogasulli	0	0	0	0	0	0	0
Cochlicella (Cochlicella) acuta	0	0	0	30	15	3	0

Species	B43	B44	B45	B46	B47	B48	B49
Cochlicella (Cochlicella) conoidea	0	0	0	0	5	0	0
Cochlicella (Prietocella) barbara	6	1	11	2	5	0	0
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	6	1	0	0	0	0
Trochoidea spl	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	0
Trichia martigena	0	0	15	0	0	0	0
Xerotrichia conspurcata	13	17	1	43	7	0	0
Xerotrichia apicina	0	0	28	6	368	8	4
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	1	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	139	12	9	0	0	13
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	11	9	0	0	0	0	1
Xerosecta (Xerosecta) promissa	25	190	2	15	0	0	95
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	0	0	0	0	0	0	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	2	0
Iberus gualtierianus alonensis	0	0	0	0	0	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	7	386	166	23	916	2	139
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	1	12	0	25	0	0	0
Otala (Otala) lactea	14	44	98	5	0	663	55
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	63	27	0	21	0	56	139

Appendix 4 (continued). Species	B50	B51	B52	B53	B54	B55	B56
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	0	0	0	0	0
Granopupa granum	0	0	0	15	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	0	0	0	0	1	0	3050
Cecilioides (Cecilioides) jani	0	0	0	6	2	0	0
Cecilioides (Cecilioides) acicula	0	0	0	0	0	0	0
Ferussacia (Ferussacia) folliculus	1	0	5	288	131	97	0
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	0	0	0	0	0	0	2
Testacella maugei	2	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	4	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	0	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	7	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	1	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	3	0	0	0	0	0	0
Milax gagates	0	0	0	0	0	0	0
Milax nigricans	33	19	0	0	10	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	0	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	3	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	1	0	0	0	0	0
Caracollina (Caracollina) lenticula	0	0	57	320	17	51	0
Gasulliella simplicula	0	0	1	0	69	0	0
Gasantena simplicata Gittenbergeria turriplana	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
Oestophora calpeana	0	2	0	0	0	0	0
Oestophora tarnieri	0	0	0	0	0	0	0
Oestophora sp1	0	0	0	0	0	0	0
Hatumia pseudogasulli Cochlicella (Cochlicella) acuta	0	0	84	558	24	2155	7

Species	B50	B51	B52	B53	B54	B55	B56
Cochlicella (Cochlicella) conoidea	0	0	131	2	55	402	6
Cochlicella (Prietocella) barbara	0	0	0	0	0	0	(
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	- (
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	(
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	(
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	(
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	(
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	(
Trochoidea sp1	0	0	0	0	0	0	82
Trochoidea sp2	0	0	0	0	0	0	(
Trochoidea sp3	0	0	0	0	0	0	(
Ponentina subvirescens	0	0	0	0	0	0	(
Trichia martigena	0	0	0	0	0	0	(
Xerotrichia conspurcata	0	0	19	0	3	54	(
Xerotrichia apicina	0	0	106	733	96	777	(
Xeroleuca vatonniana	0	0	0	0	0	0	(
Helicella huidobroi	0	0	0	0	0	0	(
Helicella? stiparum	0	0	0	0	0	0	(
Candidula gigaxii	0	0	0	0	0	0	(
Candidula intersecta	0	0	0	0	0	0	(
Candidula sp1	0	0	0	0	0	0	(
Candidula sp2	0	0	0	0	0	0	(
Cernuella (Cernuella) virgata	42	191	1	0	0	0	(
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	(
Xerosecta (Xerosecta) cespitum	54	57	0	0	0	0	(
Xerosecta (Xerosecta) promissa	62	0	7	0	0	0	1
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	(
Xerosecta sp	0	0	0	0	0	0	(
Portugala inchoata	0	0	0	0	0	0	(
Microxeromagna armillata	0	0	0	3	0	0	(
Ganula gadirana	0	1	1	0	0	0	(
Iberus gualtierianus marmoratus	0	0	0	0	0	0	(
Iberus gualtierianus alonensis	0	0	0	0	0	0	(
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	(
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	2	13	875	826	644	1736	687
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	28	0	0	0	0	0	0
Otala (Otala) lactea	32	26	1	27	79	60	83
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	9	1	7	0	0	0	0

Appendix 4 (continued). Species	B57	B58	B59	B60	B61	B62	B63
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	0	0	0	0	0	1	0
Vallonia costata	0	0	0	1	0	1	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	0	0	0	0	0	20
Granopupa granum	0	0	0	0	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	5	0	0	644	122	0	0
Cecilioides (Cecilioides) jani	49	1	0	0	0	0	0
Cecilioides (Cecilioides) acicula	0	0	0	0	1	1	0
Ferussacia (Ferussacia) folliculus	145	8	0	0	0	0	0
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	14	0	34	22	0	0	2
Testacella maugei	1	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	0	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	2	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	0	0	0	0	0	0	0
Milax gagates	0	0	0	0	0	0	0
Milax nigricans	0	0	0	0	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	0	0	0	2	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	0	59	2	124	15	0	6
Gasulliella simplicula	0	0	0	0	0	0	0
Gittenbergeria turriplana	0	0	0	0	0	0	0
Destophora barbula	0	0	0	0	0	0	0
Destophora varvata Destophora calpeana	0	0	0	0	0	0	0
Destophora catpeana Destophora tarnieri	0	0	0	0	0	0	0
	0	0	0	0	0	0	0
Destophora spl	0	0	0	0	0	0	0
Hatumia pseudogasulli Cochlicella (Cochlicella) acuta	90	71	50	161	3419	3548	1

Appendix 4 (continued). Species	B57	B58	B59	B60	B61	B62	B63
Cochlicella (Cochlicella) conoidea	0	13	123	0	0	338	0
Cochlicella (Prietocella) barbara	0	0	0	12	1	267	0
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	4	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	0	0	0	2
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	19	0	9	612	293	0	47
Xerotrichia apicina	44	47	289	301	23	140	0
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	14	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	2	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	0	92	0	0	0	0	0
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	417	0	0	0	0	0	18
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	0	0
Iberus gualtierianus alonensis	0	0	0	0	0	0	3
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	1203	212	1351	149	1356	1147	16
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	27	8	29	21	0	1	0
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	0	19	20	0	0	0
Cantareus aspersus	41	32	13	21	11	4	19

Appendix 4 (continued).	- D.(4	200					
Species	B64	B65	B66	B67	B68	B69	B70
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	0	0	0	0	0	0	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	0	3	0	0	42	0	2
Granopupa granum	0	0	0	0	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	0	0	0	0	0	0	0
Cecilioides (Cecilioides) jani	0	0	0	0	0	0	25
Cecilioides (Cecilioides) acicula	0	0	0	0	0	0	3
Ferussacia (Ferussacia) folliculus	1	1	244	1	0	0	219
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	0	0	0	16	0	0	0
Testacella maugei	0	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	0	0	0	0	0	0
Vitrea (Crystallus) contracta	0	0	0	0	0	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	0	1	0	0	0	0	0
Milax gagates	0	0	0	0	0	0	0
Milax nigricans	0	0	0	0	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	3
Lehmania valentiana	0	0	0	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	0	6	173	10	0	0	108
Gasulliella simplicula	0	0	0	0	0	0	0
Gittenbergeria turriplana	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	0
Oestophora calpeana	0	0	0	0	0	0	0
Oestophora tarnieri	0	0	0	0	0	0	0
Oestophora spl	0	0	0	0	0	0	0
Hatumia pseudogasulli	0	0	0	0	0	0	0
Cochlicella (Cochlicella) acuta	0	0	0	0	18	0	1

Appendix 4 (continued).			Large				
Species	B64	B65	B66	B67	B68	B69	B70
Cochlicella (Cochlicella) conoidea	0	0	0	0	287	0	415
Cochlicella (Prietocella) barbara	0	2	0	1	0	375	4
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	1	0	0	0
Trochoidea sp3	1	0	0	0	0	0	0
Ponentina subvirescens	1	28	3	13	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	0	3	51	0	0	0	0
Xerotrichia apicina	0	0	0	0	266	133	88
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	0	0	0	0	0	0
Cernuella (Cernuella) virgata	0	0	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	2	0	0	0	0	0	2
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	1	0	0	0
Microxeromagna armillata	0	14	140_	13	36	12	103
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	0	0
Iberus gualtierianus alonensis	0	0	0	0	0	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	0	3	113	74	182	220	62
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	1	7	6	0	0	60	161
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	0	2	0	0	0	0	24

Appendix 4 (continued). Species	B71	B72	B73	B74	B75	B76	B77
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	28	40	0	0	0	0	5
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	12	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	108	0	0	32	0	0	0
Granopupa granum	0	3	0	0	1	8	0
Truncatellina callicratis	0	30	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	1	10	0	0	12	7	0
Cecilioides (Cecilioides) jani	1	5	1	1	17	5	1
Cecilioides (Cecilioides) acicula	0	3	0	0	73	0	0
Ferussacia (Ferussacia) folliculus	110	114	3	12	14	64	7
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	2	0	31	2	13	2	0
Testacella maugei	0	0	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	36	0	0	0	2	0
Paralaoma caputspinulae	0	0	0	0	11	0	1
Vitrea (Crystallus) contracta	0	38	0	7	25	8	3
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	0	0	0	0	18	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	2
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	0	0	0	1	2	1	0
Milax gagates	3	2	0	0	0	0	0
Milax nigricans	0	1	0	0	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	2	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	26	0	11	15	8	172	12
Gasulliella simplicula	0	0	0	0	0	0	0
Gittenbergeria turriplana	381	151	0	0	141	6	0
Oestophora barbula	0	0	0	0	0	0	0
Oestophora calpeana	0	0	0	0	0	0	0
Oestophora tarnieri	0	0	0	0	0	0	0
Oestophora spl	0	0	0	0	0	0	0
Hatumia pseudogasulli	0	0	0	0	0	0	0
Cochlicella (Cochlicella) acuta	1	10	159	0	83	137	63

Appendix 4 (continued). Species	B71	B72	B73	B74	B75	B76	B77
Cochlicella (Cochlicella) conoidea	0	0	0	0	0	0	0
Cochlicella (Prietocella) barbara	180	5	287	117	0	0	152
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	0	1	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	0	0	1	0	0	0
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	747	0	132	11	9	0	48
Xerotrichia apicina	68	0	644	2	0	15	229
Xeroleuca vatonniana	0	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	0	0	0	0	0	0
Candidula sp2	0	14	0	0	- 0	0	0
Cernuella (Cernuella) virgata	0	0	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	30	0	0	0	0	1
Xerosecta (Xerosecta) promissa	11	69	86	0	41	423	9
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	0	0	0	0	0	0	0
Microxeromagna armillata	37	76	0	65	104	174	0
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	0	0
Iberus gualtierianus alonensis	0	0	0	0	0	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	46	18	934	83	76	286	605
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	130	53	133	25	94	44	62
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	87	2	29	8	21	13	3

Appendix 4 (continued).	D50	D50	Doo	DOI	Doa	Doa	DOA
Species	B78	B79	B80	B81	B82	B83	B84
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	22	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	49	0	0	0	0	1	0
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	26	0	0	0	0	0	0
Pyramidula pusilla	68	0	0	0	0	1	0
Granopupa granum	0	0	0	0	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	9	0	0_	0	0	0	0
Truncatellina cylindrica	0	2	44	0	0	9	22
Cecilioides (Cecilioides) jani	0	43	0	0	0	2	0
Cecilioides (Cecilioides) acicula	32	0	86	0	0	0	0
Ferussacia (Ferussacia) folliculus	110	11	222	0	0	23	0
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	1	0	26	24	0	0	147
Testacella maugei	0	1	0	0	0	0	0
Punctum (Punctum) pygmaeum	0	0	0	0	0	0	0
Paralaoma caputspinulae	0	4	0	0	0	0	0
Vitrea (Crystallus) contracta	120	17	35	0	0	2	1
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius	0	0	0	0	0	0	0
Oxychilus (Oxychilus) draparnaudi	2	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus	0	0	0	0	0	0	0
Oxychilus sp1	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
Parmacella (Parmacella) valencieni	0	0	1	0	0	0	0
Milax gagates	0	0	0	0	0	0	0
Milax nigricans	0	0	0	0	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	0
Lehmania valentiana	0	0	0	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	0	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	0	0	0	0	0	0	0
Caracollina (Caracollina) lenticula	87	15	37	0	0	5	0
Gasulliella simplicula	0	0	0	0	0	0	0
Gusuntena simplicata Gittenbergeria turriplana	0	0	0	0	0	0	0
Oestophora barbula	0	0	0	0	0	0	2
	0	0	0	0	0	0	0
Oestophora calpeana	0	0	0	0	0	0	0
Oestophora tarnieri	0	0	0	0	6	0	0
Oestophora sp1	0	0	0	0	0	0	0
Hatumia pseudogasulli Cochlicella (Cochlicella) acuta	11	0	33	0	0	12	0

Appendix 4 (continued). Species	B78	B79	B80	B81	B82	B83	B84
Cochlicella (Cochlicella) conoidea	0	0	0	2	0	1	0
Cochlicella (Prietocella) barbara	168	0	0	0	0	0	1
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	(
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	(
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	(
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	(
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	(
Trochoidea sp1	0	0	0	0	0	0	(
Trochoidea sp2	0	0	0	0	0	0	(
Trochoidea sp3	0	0	0	0	0	0	(
Ponentina subvirescens	0	0	0	0	2	0	(
Trichia martigena	0	0	0	0	0	0	(
Xerotrichia conspurcata	96	6	0	2	0	0	(
Xerotrichia apicina	0	1	0	0	0	0	(
Xeroleuca vatonniana	2	0	0	0	0	0	10
Helicella huidobroi	0	0	0	0	0	0	(
Helicella? stiparum	0	0	0	0	0	0	(
Candidula gigaxii	0	18	0	0	0	0	(
Candidula intersecta	0	0	0	0	2	0	(
Candidula sp1	0	0	0	17	0	0	(
Candidula sp2	0	0	0	0	- 0	0	0
Cernuella (Cernuella) virgata	0	0	57	0	0	0	(
Xerosecta (Xerosecta) adolfi	0	- 0	0	0	0	0	(
Xerosecta (Xerosecta) cespitum	6	33	24	0	0	0	0
Xerosecta (Xerosecta) promissa	13	27	91	0	0	0	(
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	C
Xerosecta sp	0	31	0	0	0	0	C
Portugala inchoata	0	0	0	38	137	9	79
Microxeromagna armillata	27	0	296	0	0	30	51
Ganula gadirana	0	0	0	0	0	0	(
Iberus gualtierianus marmoratus	0	0	0	0	0	0	
Iberus gualtierianus alonensis	0	0	0	0	0	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	345	187	523	37	0	1131	23
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	73	193	123	31	0	56	38
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	17	20	26	26	0	0	15

Appendix 4 (continued). Species	B85	B86	B87	B88	B89	B90	B91
Acicula norrisi	0	0	0	0	0	0	0
Leonia mamillaris	0	0	0	0	0	0	0
Carychium minimum	0	0	0	0	0	0	0
Hypnophila malagana	0	0	0	0	0	0	0
Lauria (Lauria) cylindracea	32	0	0	9	1074	0	1
Vallonia costata	0	0	0	0	0	0	0
Vallonia excentrica	0	0	0	0	0	0	0
Vallonia pulchella	0	0	0	0	0	0	0
Pyramidula pusilla	99	82	0	10	124	3	56
Granopupa granum	0	0	0	0	0	0	0
Truncatellina callicratis	0	0	0	0	0	0	0
Truncatellina claustralis	0	0	0	0	0	0	0
Truncatellina cylindrica	103	0	2	1	172	2	174
Cecilioides (Cecilioides) jani	0	0	0	0	0	0	0
Cecilioides (Cecilioides) acicula	0	0	0	0	0	0	0
Ferussacia (Ferussacia) folliculus	0	0	0	0	0	23	12
Hohenwartiana eucharista	0	0	0	0	0	0	0
Rumina decollata	0	0	3	14	4	83	0
Testacella maugei	0	0	0	0	0	0	0
	0	1	0	0	0	0	0
Punctum (Punctum) pygmaeum Paralaoma caputspinulae	0	0	0	1	0	0	0
	3	56	0	2	-86	0	0
Vitrea (Crystallus) contracta	0	0	0	0	1	0	0
Euconulus (Euconulus) fulvus	0	0	0	0	0	0	0
Mastus pupa	0	0	0	0	0	0	0
Oxychilus (Oxychilus) cellarius Oxychilus (Oxychilus) draparnaudi	0	0	0	0	0	51	5
	0	0	0	0	0	0	0
Oxychilus (Oxychilus) hydatinus Oxychilus spl	0	0	0	0	0	0	0
Oxychilus sp2	0	0	0	0	0	0	0
Oxychilus sp3	0	0	0	0	0	0	0
	0	0	0	3	0	0	0
Parmacella (Parmacella) valencieni Milax gagates	0	0	0	0	0	0	0
	0	0	0	0	0	0	1
Milax nigricans	0	0	0	2	0	0	0
Limax (Limacus) flavus	0	0	0	0	0	0	4
Lehmania valentiana	0	0	0	0	0	0	0
Deroceras (Deroceras) panormitanum	0	0	0	0	0	0	0
Deroceras (Agriolimax) reticulatum	0	5	0	0	0	0	0
Deroceras (Agriolimax) nitidum	0	0	0	0	0	0	0
Deroceras (Agriolimax) ponsonbyi	0	0	0	0	0	0	0
Sphincterochila (Albea) candidissima	0	0	0	0	0	0	0
Sphnincterochila (Cariosula) baetica	0	0	0	0	0	0	0
Geomalacus malagensis	1	9	0	287	39	29	30
Caracollina (Caracollina) lenticula	0	0	0	0	0	0	0
Gasulliella simplicula	0	0	0	0	0	0	0
Gittenbergeria turriplana	0	2	0	49	1	0	0
Oestophora barbula	0	0	0	0	0	0	
Oestophora calpeana	_	0	0	0	-		0
Oestophora tarnieri	0	0	0	0	0	0	0
Oestophora spl		0	0		0	0	0
Hatumia pseudogasulli	66	0	0	3	5	0	0

Appendix 4 (continued).					July 19 H		
Species	B85	B86	B87	B88	B89	B90	B91
Cochlicella (Cochlicella) conoidea	0	0	0	0	0	0	0
Cochlicella (Prietocella) barbara	29	0	0	17	100	0	28
Trochoidea (Trochoidea) elegans	0	0	0	0	0	0	0
Trochoidea (Trochoidea) pyradimata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) barceloi	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) derogata	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) murcica	0	0	0	0	0	0	0
Trochoidea (Xerocrassa) jimenensis	0	0	0	0	0	0	0
Trochoidea sp1	0	0	0	0	0	0	0
Trochoidea sp2	0	0	3	0	0	0	0
Trochoidea sp3	0	0	0	0	0	0	0
Ponentina subvirescens	0	2	0	0	0	2	29
Trichia martigena	0	0	0	0	0	0	0
Xerotrichia conspurcata	0	1	0	0	0	0	0
Xerotrichia apicina	0	0	0	0	36	0	0
Xeroleuca vatonniana	66	0	0	0	0	0	0
Helicella huidobroi	0	0	0	0	0	0	0
Helicella? stiparum	0	0	0	0	0	0	0
Candidula gigaxii	0	0	0	0	0	0	0
Candidula intersecta	0	0	0	0	0	0	0
Candidula sp1	0	3	0	0	0	12	0
Candidula sp2	0	0	0	0	- 5	0	0
Cernuella (Cernuella) virgata	0	0	0	0	0	0	0
Xerosecta (Xerosecta) adolfi	0	0	0	0	0	0	0
Xerosecta (Xerosecta) cespitum	0	0	0	0	0	0	0
Xerosecta (Xerosecta) promissa	0	0	0	0	0	0	0
Xerosecta (Xerosecta) reboudiana	0	0	0	0	0	0	0
Xerosecta sp	0	0	0	0	0	0	0
Portugala inchoata	9	13	3	19	21	3	17
Microxeromagna armillata	99	0	0	240	38	19	312
Ganula gadirana	0	0	0	0	0	0	0
Iberus gualtierianus marmoratus	0	0	0	0	0	0	0
Iberus gualtierianus alonensis	0	0	0	0	0	0	0
Iberus gualtierianus gualtierianus	0	0	0	0	0	0	0
Iberus gualtierianus globulosus	0	0	0	0	0	0	0
Theba pisana	128	0	0	67	375	114	288
Theba gittenbergeri	0	0	0	0	0	0	0
Theba subdentata helicella	0	0	0	0	0	0	0
Pseudotachea litturata	0	0	0	0	0	0	0
Otala (Otala) lactea	41	2	0	138	95	251	132
Otala (Otala) punctata	0	0	0	0	0	0	0
Eobania vermiculata	0	0	0	0	0	0	0
Cantareus aspersus	7	1	0	47	28	22	21

Appendix 5. The environmental variables at the Biogeographical Sites. See Appendix 1 for site numbering and details.

Abbreviations used in Appendix 5:

Abbreviation	Environmental variable name, classification and unit of mesaurement
ALTI	Altitude: Metres above sea level (Using altimeter)
DEPO	Geology (rock/deposit type): Sensu Roberts, 1989; Anon., 1994
GEOL	Geological period: Sensu Black, 1998; Lincoln et al., 1998
RAIN	Rainfall: Annual mean (mm)
SANN	Sunshine: Annual mean (hours/day)
SJAN	Sunshine-January: Monthly mean (hours/day)
SFEB	Sunshine-February: Monthly mean (hours/day)
SMAR	Sunshine-March: Monthly mean (hours/day)
SAPR	Sunshine-April: Monthly mean (hours/day)
SMAY	Sunshine-May: Monthly mean (hours/day)
SJUN	Sunshine-June: Monthly mean (hours/day)
SJUL	Sunshine-July: Monthly mean (hours/day)
SAUG	Sunshine-August: Monthly mean (hours/day)
SSEP	Sunshine-September: Monthly mean (hours/day)
SOCT	Sunshine-October: Monthly mean (hours/day)
SNOV	Sunshine-November: Monthly mean (hours/day)
SDEC	Sunshine-December: Monthly mean (hours/day)
TANN	Temperature: Annual mean (°C)
TJAN	Temperature-January: Monthly mean (°C)
TJUL	Temperature-July: Monthly mean (°C)
TDJA	Temperature (diurnal variation)-January: Monthly mean (°C)
TDJU	Temperature (diurnal variation)-July: Monthly mean (°C)
TD00	Temperature (mean number of days in year when temperature is less than or equal to 0°C): Annual mean (number of days)
TD20	Temperature (mean number of days in year when temperature is more than or equal to 20°C): Annual mean (number of days)
WIND	Wind: Annual mean (km/hr)
ABHU	Absolute humidity: Annual mean (g/m ³)

Site No.	Site Name	ALTI	DEPO	GEOL	RAIN	SANN	SJAN	SFEB	SMAR	SAPR
B1	Guardamar del Segura, Spain	40	9	12	300	7.9	5.5	6.4	6.7	8.2
B2	Torrevieja, Spain	50	10	15	300	7.6	5.5	6.4	6.7	7.9
В3	El Pilar de la Horadada, Spain	80	10	15	300	7.6	5.5	6.4	6.4	7.9
B4	Los Alcázares, Spain	20	10	15	300	7.6	5.5	6.4	6.4	7.9
B5	Cabo de Palos, Spain	35	9	- 11	300	8.2	5.5	6.4	6.4	7.9
B6	Portman, Spain	75	2	1	300	8.2	5.8	6.4	7.0	8.2
B7	Cartagena, Spain	25	2	2	300	8.2	5.8	6.4	7.0	8.2
B8	La Azohia, Spain	50	2	2	300	8.2	5.8	6.4	7.0	8.2
B9	Mazarrón, Spain	80	10	15	300	8.2	5.8	6.4	7.0	8.2
B10	Puntas del Calnegre, Spain	45	2	1	300	8.2	5.8	6.4	7.0	8.2
B11	Cabo Cope, Spain	3	2	1	300	8.2	5.8	6.4	7.0	8.2
B12	Aguilas, Spain	25	2	2	300	8.2	5.8	6.4	7.0	8.2
B13	San Juan de los Terreros, Spain	50	10	14	300	8.2	5.8	6.4	7.0	8.2
B14	Villaricos, Spain	15	2	1	300	8.2	5.8	6.4	7.0	8.2
B15	Garrucha, Spain	10	10	15	300	8.2	5.8	6.4	7.0	8.2
B16	Playa de Macenas, Spain	40	9	11	300	8.2	5.8	6.4	7.0	8.2
B17	Punta de los Muertos, Spain	100	9	11	300	8.2	5.8	6.4	7.0	8.2
B18	Las Negras, Spain	35	9	11	300	8.2	5.8	6.4	7.0	8.2
B19	El Pozo de los Frailes, Spain	80	9	11	300	8.2	5.8	6.4	7.0	8.2
B20	Cabo de Gata, Spain	20	9	11	300	8.2	5.8	6.4	7.0	8.2
B21	Retamar, Spain	50	10	15	300	8.2	5.8	6.4	7.0	8.2
B22	Almeria, Spain	30	10	15	400	7.9	5.8	6.4	7.0	7.9
B23	Roquetas de Mar, Spain	125	10	15	400	7.9	5.8	6.4	6.7	7.9
B24	Punta del Sabinar, Spain	20	10	15	400	7.9	5.8	6.4	6.7	7.9
B25	Guardias Viejas, Spain	10	10	14	400	7.9	5.8	6.4	6.7	7.9
B26	Adra, Spain	95	2	2	500	7.9	5.8	6.4	6.7	7.9
B27	La Rabita, Spain	25	2	2	500	7.9	5.8	6.4	6.7	7.9

Site No.	Site Name	ALTI	DEPO	GEOL	RAIN	SANN	SJAN	SFEB	SMAR	SAPR
B28	La Guapa, Spain	110	2	2	500	7.9	5.8	6.4	6.7	7.9
B29	Calahonda, Spain	65	2	2	500	7.9	5.8	6.4	6.7	7.9
B30	Torrenueva, Spain	15	10	14	500	7.9	5.8	6.4	6.7	7.9
B31	Torrecuevas, Spain	275	2	2	600	7.9	5.8	6.4	6.7	7.9
B32	Lagos, Spain	35	2	2	600	7.9	5.8	6.4	6.7	7.9
B33	Torrex, Spain	110	2	2	600	7.9	5.8	6.4	6.7	7.9
B34	Torre del Mar, Spain	25	9	12	600	7.9	5.8	6.4	6.7	7.9
B35	Benajarafe, Spain	25	2	1	600	7.9	5.8	6.4	6.7	7.9
B36	Benagalbon, Spain	95	2	1	600	7.9	5.8	6.4	6.7	7.9
B37	Malaga, Spain	50	9	1	600	7.9	5.8	6.1	6.7	7.9
B38 B39	Torremolinos, Spain Fuengirola, Spain	45	2	12	600	7.9	5.5	6.1	6.7	7.9
B40	Los Jarales, Spain	10	2	1	700	7.9	5.5 5.5	6.1	6.7	7.9
B41	Marbella, Spain	15	6	7	700	7.9	5.5	6.1	6.7	7.6
B42	San Pedro de Alcantara, Spain	20	6	7	700	7.9	5.2	5.8	6.7	7.6
B43	Rio del Padrón, Spain	1	9	10	700	7.9	5.2	5.8	6.7	7.6
B44	Casares, Spain	40	6	7	700	7.9	5.2	5.8	6.7	7.6
B45	Cala Sardina, Spain	20	9	10	700	7.9	5.2	5.8	6.7	7.6
B46	Sotogrande, Spain	3	9	12	1000	7.6	5.2	5.8	6.4	7.6
B47	La Línea, Spain	10	9	10	1000	7.6	5.2	5.8	6.4	7.6
B48	Deadman's Beach, Gibraltar	25	5	6	1000	7.6	5.2	5.8	6.4	7.6
B49	Getares, Spain	20	10	15	1000	7.6	5.2	5.8	6.4	7.3
B50	Punta del Carnero, Spain	30	8	9	1200	7.6	5.2	5.8	6.1	7.3
B51	Punta del Cabrito, Spain	340	6	7	1200	7.6	5.2	5.8	6.1	7.3
B52	Rio Jara, Spain	1	7	8	1200	7.6	5.2	5.8	6.4	7.3
B53	Punta Camarinal, Spain	10	9	11	1200	8.2	5.2	5.8	6.7	7.9
B54	Zahara de los Atunes, Spain	10	9	11	1000	8.2	5.5	6.1	6.7	7.9
B55	Barbate, Spain	2	10	15	1000	8.5	5.5	6.1	7.0	7.9
B56	Cabo de Trafalgar, Spain	30	10	15	600	8.5	5.5	6.1	7.0	8.2
B57	Conil de la Frontera, Spain	40	9	11	600	8.5	5.5	6.1	7.0	8.2
B58	Chiclana de la Frontera, Spain	10	4	4	600	8.5	5.5	6.1	7.0	8.2
B59	Cadiz, Spain	2	9	12	600	8.5	5.5	6.1	7.0	8.8
B60	Rota, Spain	10	9	12	600	8.2	4.9	6.1	6.7	8.8
B61	Chipiona, Spain	3	10	15	600	8.2	4.9	6.1	6.7	8.8
B62	Sanlúcar de Barrameda, Spain	2	9	13	600	8.2	4.9	6.1	6.7	8.8
B63	Torre de la Higuera, Spain	10	10	15	600	8.2	4.9	6.1	6.7	8.8
B64	Torre del Oro, Spain	15	10	15	600	8.2	4.9	6.1	6.7	8.8
B65 B66	Mazagon, Spain Punta Umbria, Spain	10	10	15	600	8.2	4.9	5.8	6.7	8.8
B67	El Rompido, Spain	10	9	13	600	8.5	4.9	5.8	7.0	9.1
B68	Isla Cristina, Spain	10	10	15	600	8.5	4.9	5.8	6.7	9.1
B69	Monte Gordo, Portugal	2	9	11	650	8.5	4.9	5.8	6.7	9.1
B70	Tavira, Portugal	2	10	15	650	8.5	4.9	5.8	6.7	9.1
	Torre de Ares, Portugal	2	10	15	650	8.5	4.9	5.8	6.7	9.1
B72	Olhão, Portugal	50	10	15	650	8.5	4.9	5.8	6.7	9.1
B73	Faro, Portugal	5	10	15	650	8.5	4.9	5.8	6.7	9.1
B74	Vale do Lobo, Portugal	25	10	14	650	8.5	4.9	5.8	6.7	9.1
B75	Albufeira, Portugal	20	5	6	700	8.5	4.9	5.8	6.7	9.1
B76	Armação de Pera, Portugal	40	9	11	650	8.5	4.9	5.8	6.7	9.1
B77	Portimão, Portugal	2	9	11	650	8.5	4.9	5.8	6.7	8.5
B78	Luz, Portugal	20	9	12	750	8.5	4.9	5.8	6.7	8.5
B79	Burgau, Portugal	135	6	7	750	8.5	4.9	5.8	6.7	8.5
B80	Salema, Portugal	55	4	4	750	8.5	4.6	5.8	6.7	8.5
B81	Cabo São Vicente, Portugal	130	5	6	850	7.9	4.6	5.5	6.4	8.2
B82	Vila do Bispo, Portugal	90	3	3	850	7.9	4.6	5.5	6.4	8.2
B83	Carrapateira, Portugal	75	10	15	700	7.9	4.6	5.5	6.4	8.2
B84	Praia da Carriagem, Portugal	55	10	15	750	7.9	4.6	5.5	6.4	8.2
B85	Odeceixe, Portugal	80	3	3	750	7.9	4.6	5.5 5.5	6.4	8.2
B86	Zambujeira do Mar, Portugal	70	3	3	750 750	7.9	4.6	5.5	6.4	8.2
B87	Cabo Serdão Cavaleiro, Portugal	75	3	13	700	7.9	4.6	5.5	6.4	8.2
B88	Milfontes, Portugal	55	9	15	750	7.9	4.6	5.5	6.4	8.2
B89	Porto Covo, Portugal	15	10	5	750	7.9	4.6	5.5	6.4	8.2
B90	Sines, Portugal Lagoa de Santo André, Portugal	20	1	5	700	7.9	4.6	5.5	6.4	8.2
B91					700	1.1	1.0	2.0	U.T	0.2

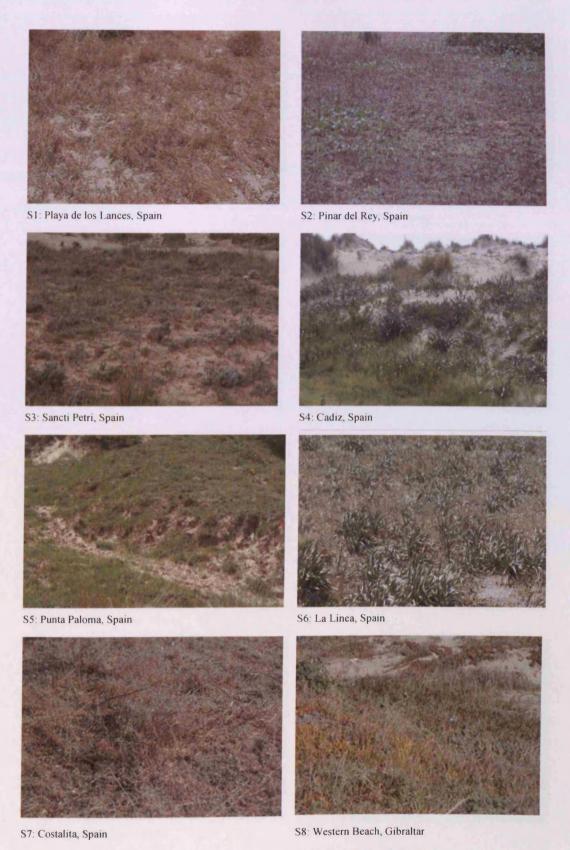
Site No.	Site Name	SMAY	SJUN	SJUL	SAUG	SSEP	SOCT	SNOV	SDEC	TANN
B1	Guardamar del Segura, Spain	9.7	10.6	10.9	10.0	7.9	6.7	6.1	5.5	16
B2	Torrevieja, Spain	9.7	10.6	10.6	10.0	7.6	6.4	5.8	5.2	16
B3	El Pilar de la Horadada, Spain	9.7	10.3	10.6	9.7	7.6	6.4	5.8	5.2	16
B4	Los Alcázares, Spain	9.7	10.3	10.6	9.7	7.6	6.4	5.8	5.2	16
B5	Cabo de Palos, Spain	9.7	10.3	10.6	9.7	7.6	6.4	5.8	5.2	16
B6	Portman, Spain	9.7	10.9	10.9	9.7	7.6	6.7	6.1	5.5	16
B7	Cartagena, Spain	9.7	10.9	11.5	10.3	7.6	6.7	6.1	5.5	16
B8	La Azohia, Spain	9.7	10.9	11.5	10.3	7.9	6.7	6.1	5.5	16
B9	Mazarrón, Spain	9.7	10.9	11.5	10.3	8.2	6.7	6.1	5.5	16
B10	Puntas del Calnegre, Spain	9.7	10.9	11.5	10.6	8.2	6.7	6.1	5.5	16
B11	Cabo Cope, Spain	9.7	10.9	11.5	10.6	8.2	6.7	6.1	5.5	16
B12	Aguilas, Spain	9.7	10.9	11.5	10.6	8.2	6.7	6.1	5.5	16
B14	San Juan de los Terreros, Spain Villaricos, Spain	9.7	10.9	11.5	10.6	8.2	6.7	6.1	5.5	16
B15	Garrucha, Spain	9.7	10.9	11.5	10.6	8.2	6.7	6.1	5.5	18
B16	Playa de Macenas, Spain	9.7	10.9	11.5	10.6	8.2	6.7	6.1	5.5	18
B17	Punta de los Muertos, Spain	9.7	10.9	11.5	10.6	8.2	6.7	6.1	5.5	18
B18	Las Negras, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B19	El Pozo de los Frailes, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B20	Cabo de Gata, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B21	Retamar, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B22	Almeria, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B23	Roquetas de Mar, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B24	Punta del Sabinar, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B25	Guardias Viejas, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B26	Adra, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B27	La Rabita, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B28	La Guapa, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B29	Calahonda, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B30	Torrenueva, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B31	Torrecuevas, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B32	Lagos, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B33	Torrex, Spain	9.7	10.9	11.5	10.6	8.5 8.5	6.7	6.1	5.5	18
B34	Torre del Mar, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.5	18
B35	Benajarafe, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.2	18
B36	Benagalbon, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.2	18
B37	Malaga, Spain	9.7	10.9	11.5	10.6	8.5	6.7	6.1	5.2	18
B38	Torremolinos, Spain	9.7	10.6	11.5	10.6	8.5	6.7	6.1	5.2	18
B39	Fuengirola, Spain	9.7	10.6	11.5	10.6	8.5	6.7	6.1	5.2	18
B40	Los Jarales, Spain	9.7	10.6	11.5	10.6	8.5	6.7	6.1	5.2	18
B41 B42	Marbella, Spain San Pedro de Alcantara, Spain	9.4	10.3	11.5	10.6	8.5	6.7	6.1	5.2	18
B43	Rio del Padrón, Spain	9.4	10.3	11.5	10.6	8.5	6.7	6.1	5.2	18
	Casares, Spain	9.4	10.3	11.2	10.6	8.5	6.7	6.1	5.2	18
B45	Cala Sardina, Spain	9.4	10.3	11.2	10.6	8.5	6.7	6.1	5.2	18
B46	Sotogrande, Spain	9.4	10.3	11.2	10.3	8.5	7.0	5.8	4.9	18
B47	La Línea, Spain	9.4	10.3	11.2	10.3	8.5	7.0	5.5	4.9	18
B48	Deadman's Beach, Gibraltar	9.4	10.3	11.2	10.3	8.5	7.0	5.8	4.9	18
B49	Getares, Spain	8.8	10.3	11.8	10.3	8.2	7.0	5.8	4.9	18
B50	Punta del Carnero, Spain	8.8	10.3	11.8	10.3	8.2	7.0	5.8	4.9	18
B51	Punta del Cabrito, Spain	9.1	10.3	11.8	10.6	8.2	7.0	6.1	4.9	18
B52	Rio Jara, Spain	9.4	10.6	11.8	10.9	8.2	7.0	6.1	5.2	18
B53	Punta Camarinal, Spain	9.7	11.2	11.8	11.2	8.8	7.0	6.1	5.2	18
B54	Zahara de los Atunes, Spain	9.7	11.2	12.1	11.2	8.8	7.3	6.1	5.2	18
B55	Barbate, Spain	9.7	11.2	12.1	11.2	9.1	7.3	6.1	5.2	18
B56	Cabo de Trafalgar, Spain	9.7	11.2	12.1	11.2	9.1	7.3	6.1	5.2	18
B57	Conil de la Frontera, Spain	9.7	11.2	12.1	11.2	9.1	7.3	6.1	5.2	18
B58	Chiclana de la Frontera, Spain	9.7	11.2	12.1	11.2	9.1	7.3	6.1	5.2	18
B59	Cadiz, Spain	9.7	11.2	12.1	11.2	9.1	7.3	6.1	5.2	18
B60	Rota, Spain	9.7	11.2	12.1	11.5	9.1				18
B61	Chipiona, Spain	10.0	11.2	12.1	11.5	9.1	7.3	6.1	5.2	18
B62	Sanlúcar de Barrameda, Spain	10.0	11.2	12.1	11.5	9.1	7.3	6.1	5.2	18
	Torre de la Higuera, Spain	10.0	117		117	7.1	1.0	0.1	0.2	10

Site No.	Site Name	SMAY	SJUN	SJUL	SAUG	SSEP	SOCT	SNOV	SDEC	TANN
B65	Mazagon, Spain	10.0	11.2	12.1	11.5	9.1	7.3	5.5	5.2	18
B66	Punta Umbria, Spain	10.0	11.2	12.1	11.5	9.1	7.3	5.5	5.2	18
B67	El Rompido, Spain	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	18
B68	Isla Cristina, Spain	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	18
B69	Monte Gordo, Portugal	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	18
B70	Tavira, Portugal	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	16
B71	Torre de Ares, Portugal	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	16
B72	Olhão, Portugal	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	16
B73	Faro, Portugal	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	16
B74	Vale do Lobo, Portugal	10.6	11.2	12.4	11.8	9.1	7.3	5.5	5.2	16
B75	Albufeira, Portugal	10.6	10.9	12.4	11.8	8.8	7.3	5.5	5.2	16
B76	Armação de Pera, Portugal	10.6	10.9	12.4	11.8	8.8	7.3	5.5	5.5	16
B77	Portimão, Portugal	10.6	10.9	12.4	11.8	8.8	7.3	5.5	5.5	16
B78	Luz, Portugal	10.6	10.9	12.4	11.5	8.8	7.3	5.2	5.5	16
B79	Burgau, Portugal	10.6	10.9	12.4	11.5	8.8	7.0	5.2	5.5	16
B80	Salema, Portugal	10.6	10.9	12.4	11.5	8.8	7.0	5.2	5.5	16
B81	Cabo São Vicente, Portugal	10.3	10.9	12.1	11.5	8.2	6.7	4.9	5.5	16
B82	Vila do Bispo, Portugal	10.0	10.9	12.1	11.5	8.5	6.7	4.9	5.2	16
B83	Carrapateira, Portugal	10.0	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B84	Praia da Carriagem, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B85	Odeceixe, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B86	Zambujeira do Mar, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B87	Cabo Serdão Cavaleiro, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B88	Milfontes, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B89	Porto Covo, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B90	Sines, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
B91	Lagoa de Santo André, Portugal	10.3	10.9	12.1	11.5	8.8	6.7	4.9	5.2	16
1013	Coefficient of Variation (%)	8.5	2.8	4.3	5.5	4.7	4.3	6.9	3.8	5.8

Appendix 5: The environmental variables at the Biogeographical Sites

Site No.	Site Name	TJAN	TJUL	TDJA	TDJU	TD00	TD20	WIND	ABHU
B1	Guardamar del Segura, Spain	10	24	10	10	10	30	15	11
B2	Torrevieja, Spain	10	24	10	10	10	30	15	11
В3	El Pilar de la Horadada, Spain	10	24	10_	10	10	30	15	11
B4	Los Alcázares, Spain	10	24	10	10	10	30	15	11
B5	Cabo de Palos, Spain	10	24	10	10	10	30	15	11
B6	Portman, Spain	10	24	10	10	10	30	15	11
B7	Cartagena, Spain	10	24	10	10	10	30	15	11
B8	La Azohia, Spain	10	24	10	12	10	30	15	11
B9	Mazarrón, Spain	10	24	10	12	10	30	15	11
B10	Puntas del Calnegre, Spain	10	24	10	12	10	30	15	11
B11	Cabo Cope, Spain	10	24	10	12	10	30	15	11
B12 B13	Aguilas, Spain	10	24	10	10	10	30	15	11
B14	San Juan de los Terreros, Spain Villaricos, Spain	10	24	10	10	10	30	15	11
B15	Garrucha, Spain	10	24	10	10	10	30	15	11
B16	Playa de Macenas, Spain	10	24	10	10	10	30	15	11
B17	Punta de los Muertos, Spain	10	24	10	10	10	30	15	11
B18	Las Negras, Spain	12	24	8	10	10	30	15	11
B19	El Pozo de los Frailes, Spain	12	24	8	10	10	30	15	11
B20	Cabo de Gata, Spain	12	24	8	10	1	50	15	12
B21	Retamar, Spain	12	24	8	10	1	50	15	12
B22	Almeria, Spain	12	24	8	10	1	50	15	12
B23	Roquetas de Mar, Spain	12	24	8	10	1	50	15	12
B24	Punta del Sabinar, Spain	12	24	8	10	1	50	15	12
B25	Guardias Viejas, Spain	12	24	8	10	1	50	15	12
B26	Adra, Spain	10	24	8	10	1	- 50	15	11
B27	La Rabita, Spain	10	24	8	10	1	50	15	11
B28	La Guapa, Spain	10	24	8	10	1	50	15	11
B29	Calahonda, Spain	10	24	8	10	1	50	15	11
B30	Torrenueva, Spain	10	24	8	10	1	50	15	11
B31	Torrecuevas, Spain	10	24	8	10	1	50	15	11
B32	Lagos, Spain	10	24	8	10	1	50	15	11
B33	Torrex, Spain	10	24	8	10	1	50	15	11
B34	Torre del Mar, Spain	10	24	8	10	1	50	15	11
B35	Benajarafe, Spain	10	24	8	10	1	50	15	11
B36	Benagalbon, Spain	10	24	8	10	1	50	15	11
B37	Malaga, Spain	12	24	8	10	1	50	15	11
B38	Torremolinos, Spain	12	24	8	10	1	50	15	11
B39_	Fuengirola, Spain	12	24	8	10	1	50	15	11
B40	Los Jarales, Spain	12	24	8	10	1	50	15	11
B41_	Marbella, Spain	12	24	8	10	1	50	15	11
B42	San Pedro de Alcantara, Spain	12	24	8	10	1	50	15	11
B43	Rio del Padrón, Spain	12	24	8	10	1	50	15	11
B44	Casares, Spain	12	24	8	10	1	50	15	11
B45	Cala Sardina, Spain	12	24	8	10	1	50	15	11
B46	Sotogrande, Spain	12	24	8	10	1	50	30	11
B47	La Línea, Spain	12	24	8	8	1	50	30	12
B48	Deadman's Beach, Gibraltar	12	24	8	8	1	30	30	12
B49	Getares, Spain Punta del Carnero, Spain	12	24	8	8	1	30	30	12
B50	Punta del Cabrito, Spain	12	24	8	8	1	30	30	12
B51 B52	Rio Jara, Spain	12	24	8	8	1	30	30	12
B53	Punta Camarinal, Spain	12	24	8	8	1	30	30	12
B54	Zahara de los Atunes, Spain	12	24	8	8	1	30	30	12
B55	Barbate, Spain	12	24	8	8	1	30	15	12
B56	Cabo de Trafalgar, Spain	12	24	8	8	1	30	15	12
B57	Conil de la Frontera, Spain	10	24	8	8	1	30	15	12
B58	Chiclana de la Frontera, Spain	10	24	8	10	1	50	15	11
B59	Cadiz, Spain	10	24	8	10	1	50	15	11
B60	Rota, Spain	10	24	8	10	1	50	15	11
B61	Chipiona, Spain	10	24	8	10	1	50	15	11
B62	Sanlúcar de Barrameda, Spain	10	24	8	10	1	50	15	11
B63	Torre de la Higuera, Spain	10	24	8	10	1	50	15	11
B64	Torre del Oro, Spain	10	- 24	8	10	1	50	15	11
B65	Mazagon, Spain	10	24	8	10	1	50	15	11
B66	Punta Umbria, Spain	10	24	8	10	1	50	15	11
	El Rompido, Spain	12	24	8	10	1	50	15	11

Site No.	Site Name	TJAN	TJUL	TDJA	TDJU	TD00	TD20	WIND	ABHU
B68	Isla Cristina, Spain	12	24	8	10	1	50	15	11
B69	Monte Gordo, Portugal	12	24	8	10	1	50	15	11
B70	Tavira, Portugal	12	24	8	10	1	50	15	11
B71	Torre de Ares, Portugal	12	24	8	10	1	50	15	11
B72	Olhão, Portugal	12	24	8	10	1	50	15	11
B73	Faro, Portugal	12	24	8	10	1	50	15	- 11
B74	Vale do Lobo, Portugal	12	24	8	10	1	50	15	11
B75	Albufeira, Portugal	12	24	8	10	1	50	15	11
B76	Armação de Pera, Portugal	12	24	8	10	1	50	15	11
B77	Portimão, Portugal	12	24	8	10	1	50	30	11
B78	Luz, Portugal	12	24	8	8	1	50	30	12
B79	Burgau, Portugal	12	24	8	8	1	30	30	12
B80	Salema, Portugal	12	24	- 8	8	1	30	30	12
B81	Cabo São Vicente, Portugal	12	24	8	8	1	30	30	12
B82	Vila do Bispo, Portugal	12	24	8	8	1	30	30	12
B83	Carrapateira, Portugal	12	24	8	8	1	30	30	12
B84	Praia da Carriagem, Portugal	12	24	8	8	1	30	30	12
B85	Odeceixe, Portugal	12	24	8	8	1	30	15	12
B86	Zambujeira do Mar, Portugal	12	24	8	8	1	30	15	12
B87	Cabo Serdão Cavaleiro, Portugal	10	24	8	8	1	30	15	12
B88	Milfontes, Portugal	10	24	8	10	1	50	15	- 11
B89	Porto Covo, Portugal	10	24	8	10	1	50	15	11
B90	Sines, Portugal	10	24	8	10	1	50	15	11
B91	Lagoa de Santo André, Portugal	10	24	8	10	1	50	15	11
	Coefficient of Variation (%)	9.1	0	9.5	10.3	127.6	23.6	32.4	4.4



Appendix 6. Photographs of the Habitat Structure Sites: S1 to S8. See Table 6.1 for site details.



Appendix 6 (continued). Photographs of the Habitat Structure Sites: S9 to S16. See Table 6.1 for site details.



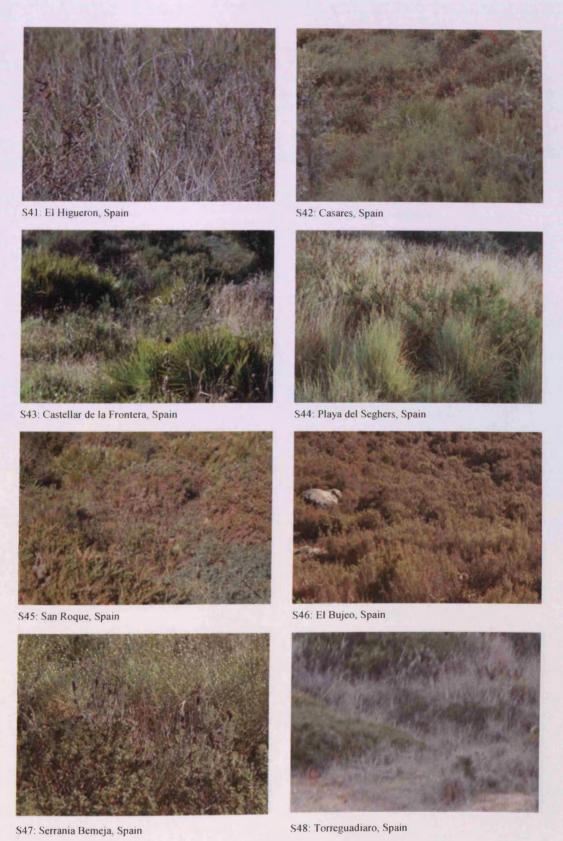
Appendix 6 (continued). Photographs of the Habitat Structure Sites: S17 to S24. See Table 6.1 for site details.



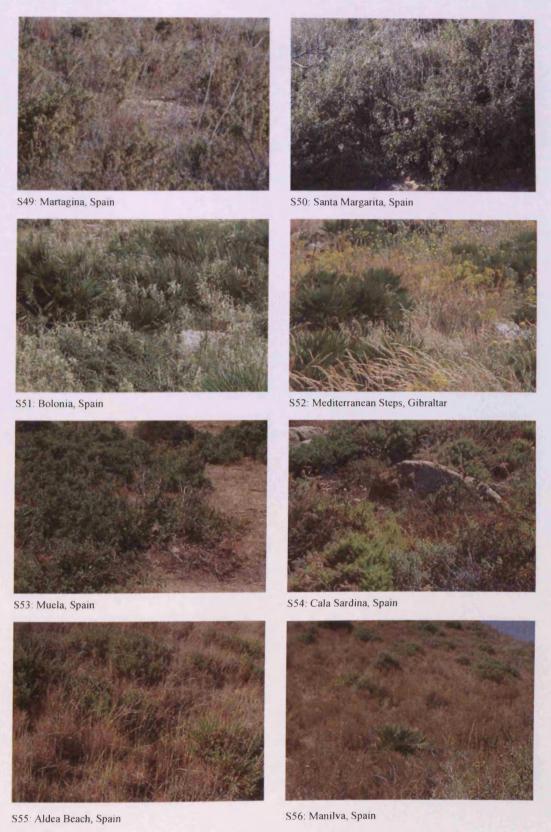
Appendix 6 (continued). Photographs of the Habitat Structure Sites: S25 to S32. See Table 6.1 for site details.



Appendix 6 (continued). Photographs of the Habitat Structure Sites: S33 to S40. See Table 6.1 for site details.

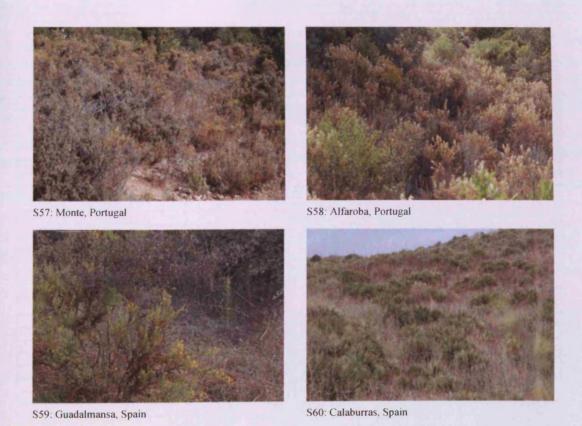


Appendix 6 (continued). Photographs of the Habitat Structure Sites: S41 to S48. See Table 6.1 for site details.



Appendix 6 (continued). Photographs of the Habitat Structure Sites: S49 to S56. See Table 6.1 for site details.

Appendix 6. Photographs of the Habitat Structure Sites



Appendix 6 (continued). Photographs of the Habitat Structure Sites: S57 to S60. See Table 6.1 for site details.

Appendix 7. Random number sequences for the Habitat Structure Sites showing the plot identities and the quadrat identities for each plot. See Section 6.4.1 for details of the method used to derive the plot and quadrat identities, and Table 6.1 for site details.

		Quadrats in:						
Site/ Sequence	Plot ID	Plot a	Plot b	Plot c	Plot d			
1	06,12,10,05	05,12,17,18,24	00,11,13,17,21	01,04,05,15,22	03,08,11,17,19			
2	13,06,14,15	05,06,11,17,21	05,15,20,21,22	01,04,16,17,19	02,08,09,11,15			
3	02,12,08,10	03,14,16,19,23	01,05,16,19,22	03,10,11,20,23	01,04,11,16,24 14,15,18,20,21			
4	00,13,07,14	08,09,11,15,21	05,08,09,13,20	02,06,07,16,21 03,09,14,19,21	01,04,11,12,23			
5	15,08,06,11	03,07,09,11,24 00,07,15,18,20	00,06,15,16,20	02,12,14,17,21	02,12,17,21,24			
<u>6</u> 7	03,04,08,15	04,08,14,18,21	02,06,09,14,20	05,08,10,17,23	03,10,14,18,21			
8	05,03,13,07	05,11,16,18,21	03,08,14,15,18	02,09,12,14,19	03,07,10,14,17			
9	00,14,07,05	11,14,17,20,21	01,02,06,12,24	03,12,15,17,20	07,08,13,16,21			
10	05,05,07,12	00,03,12,20,21	06,12,14,17,19	03,06,07,13,15	01,07,11,17,22			
11	00,06,04,00	01,08,12,14,19	01,04,06,10,16	02,07,16,19,22	10,11,13,18,20			
12	05,01,09,15	05,07,16,19,24	06,08,10,14,20	00,05,12,15,19	03,09,16,18,22			
13	04,04,12,11	04,07,15,16,21	06,09,11,18,19	00,10,19,23,24	02,05,07,16,19			
14	09,07,14,12	01,05,07,15,19	00,03,10,16,18	03,05,09,15,17	04,10,13,21,24			
15	12,09,12,07	01,03,09,15,21	02,09,15,20,23	03,07,08,16,18	00,03,07,16,21			
16	13,04,04,07	02,06,11,16,20	01,02,09,12,16	01,04,14,15,21	04,09,11,16,18			
17	04,05,13,12	08,11,14,15,21	06,07,18,19,22	02,12,19,20,23 00,05,07,15,18	00,05,11,13,17 11,13,15,18,22			
18	13,13,08,02	01,11,16,21,24	05,09,16,18,21 01,02,06,16,19	03,09,10,16,18	02,05,12,16,23			
19	09,05,12,05	09,10,15,17,21 01,06,10,16,20	02,07,09,12,16	07,11,16,20,23	04,09,13,16,21			
20	00,02,10,05	03,04,17,18,23	09,11,13,14,17	00,15,17,20,21	01,07,08,13,18			
22	05,12,12,00	03,09,12,15,20	01,04,07,16,21	02,05,08,16,22	02,08,11,13,16			
23	03,04,14,14	01,04,07,13,20	00,02,10,17,21	07,11,13,22,23	01,10,16,18,21			
24	07,02,08,01	03,06,09,15,18	04,10,15,16,22	03,06,11,13,17	06,10,11,13,17			
25	00,02,10,02	03,09,14,19,22	00,08,09,18,21	02,05,07,12,16	07,10,16,18,21			
26	12,11,00,12	00,11,19,21,24	11,12,16,19,21	02,11,15,19,22	04,08,16,17,20			
27	15,01,14,10	09,11,14,20,24	02,04,08,13,18	04,08,11,14,18	04,07,10,15,20			
28	06,05,12,10	00,03,05,11,13	01,03,12,18,22	05,10,13,21,22	03,08,14,28,20			
29	03,10,03,10	00,12,16,19,23	02,05,08,14,19	04,07,11,14,17	03,09,12,17,22			
30	11,07,10,12	02,04,09,15,18	03,11,14,21,23	04,08,15,16,21 00,08,11,18,20	04,06,19,20,23 06,13,19,20,23			
31	05,09,06,10	06,13,19,21,23	06,13,19,20,24 08,10,11,14,22	00,03,10,13,24	03,11,14,19,21			
32	01,00,04,15	02,08,12,20,23 01,10,12,15,20	05,10,12,16,18	00,12,20,23,24	00,04,09,17,19			
33 34	09,02,11,14	02,09,18,21,24	06,07,09,11,22	01,10,12,15,17	05,13,15,21,22			
35	04,10,00,12	03,06,13,17,19	03,04,12,16,20	07,12,15,18,22	04,08,10,15,18			
36	13,08,14,15	01,12,14,18,21	08,10,18,22,24	01,05,08,14,15	03,07,13,16,18			
37	10.00,13.08	05,09,16,19,24	01,07,11,14,20	03,04,09,12,16	02,08,12,17,19			
38	04,00,15,05	03,05,15,20,22	05,12,15,18,20	02,13,15,18,22	01,05,06,15,20			
39	07,11,10,05	06,09,14,18,19	00,05,11,16,18	12,15,20,22,24	02,04,08,16,21			
40	11,10,05,01	06,09,15,20,22	01,11,13,15,19	02,04,07,14,20	03,09,10,18,21			
41	04,09,05,03	07,10,12,16,17	02,07,13,19,21	13,16,21,22,24	00,01,06,11,13			
42	03,04,00,03	03,08,12,17,22	06,11,14,16,20	01,03,07,12,18	00,13,14,17,22			
43	09,15,12,11	11,13,16,19,21	03,10,16,17,22 03,10,16,17,22	08,10,13,17,19 08,10,13,17,19	02,12,18,19,20			
44	09,15,12,11	11,13,16,19,21	03,10,16,17,22	11,15,17,18,20	00,01,07,10,24			
45	15,15,09,10	08,09,15,17,24 05,11,15,19,22	03,10,13,16,18	04,06,11,17,24	04,06,17,18,21			
46	15,03,13,13	00,07,14,16,17	03,10,13,10,18	00,05,11,14,23	01,02,08,15,21			
47	13,10,14,11 06,09,09,07	12,14,17,20,21	02,09,13,16,19	07,09,15,18,21	05,08,15,20,22			
48	06,09,09,07	04,12,14,16,22	01,02,09,14,22	01,04,13,16,19	03,14,17,19,23			
50	06,07,11,10	06,07,15,19,21	07,08,14,16,19	01,04,09,17,20	02,03,09,14,17			
51	10,09,02,11	00,13,18,19,23	00,01,04,10,19	07,12,16,18,21	00,08,10,18,22			
52	08,11,13,06	06,10,13,21,24	00,07,09,14,17	03,09,10,15,24	01,02,07,11,18			
53	02,06,14,13	04,09,10,15,18	04,05,09,11,13	00,04,07,13,14	02,05,11,14,16			
54	07,01,11,14	04,05,07,12,17	03,11,12,15,23	04,14,18,20,23	09,14,15,19,23			
55	14,05,14,13	02,07,14,17,24	00,08,09,14,19	02,03,08,11,15	03,09,11,13,23			
56	07,04,10,09	00,03,06,14,17	01,05,13,19,22	00,02,08,14,16	05,09,19,21,24 07,09,13,16,20			
57	09,12,05,02	03,09,12,13,19	01,04,13,17,21	04,06,13,19,22 06,11,19,21,24	10,15,16,20,24			
58	13,07,14,15	05,07,10,15,20	02,09,10,17,19 06,10,13,17,21	01,04,06,14,18	00,13,15,21,23			
59	06,09,06,02	04,07,14,15,20	05,14,18,21,32	03,09,10,14,17	00,05,08,14,19			
60	07,03,10,10	05,06,13,18,22	05,17,10,21,52	1 00,00,10,17,17	,,,,,,			

Appendix 8. Characterization of the components of the plants.

Most plants are composed of a hierarchy of components (also called modules or subunits) that can be used to analyze plant growth or compare different species (Waller, 1986; Klein and Klein, 1988) as well as for determining utilization of plants by herbivores (Lawton, 1983; Harper, 1985; Price *et al.*, 1995). The positions of the molluscs on the vegetation, using a simple classification of plant components to record positions (Table), were recorded as described in Section 6.5.

The classification system used for the characterization of the components of the plants.

plant type	components					
green grass	entire plant					
dry grass	entire plant					
annual	main stem, side stem, leaf					
nerbaceous	main stem, side stem, leaf					
hrub	main stem, side stem, leaf					
ree	main stem, side stem, leaf					

Appendix 9. Characterization of shingle, stones and rocks. See Table 6.5 for all environmental variables including measurement/scoring criteria and notes.

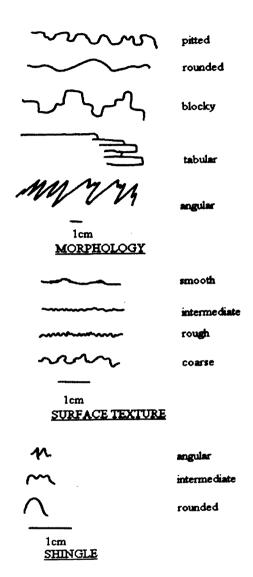
The types of shingle, and the morphology and surface texture of stones and rocks were characterized using criteria based on Trudgill's (1988) system (Figure). To remove as much as possible any bias in the selection of these for analysis, two pieces of shingle, and two stones and rocks were chosen from the four corners and the centre (for a total of ten measures each). In cases where these regions of the quadrat had no, or insufficient samples, the position nearest any of the points was used in each case.

The surface hardness of stones and rocks was assessed using a pocketknife where surfaces easily scored were *soft*, those scored only with considerable effort were *intermediate* and those resistant to scoring were *hard*. Rocks were tested for the presence of calcium carbonate (CaCO₃) using 0.1 Molar hydrochloric acid; 0.1ml of the acid was added to the sample *in situ* and effervescence, indicating the liberation of carbon dioxide gas (CO₂), was accepted as evidence of calcium carbonate in the sample (Bandtock and Hanson, 1974).

An assessment was made of the percentage of rocks that were embedded in the substratum. Rocks were recorded as embedded if (a) they were not possible to overturn, even with considerable manual force, or (b) if they formed part of a rock outcrop, or large boulder (generally greater than 0.5m in diameter). This assessment is dependent on the strength of the fieldworker but is standardized in this study across sites because all assessments were done by one worker (the author).

Appendix 9. Characterization of shingle, stone and rocks

The morphology and surface texture types used to characterize stones and rocks; the shingle types are also shown (based on Trudgill, 1988).



Appendix 10. Species at the Habitat Structure Sites: the number of sites of each habitat type at which each species was present.

Species	Sand	Steppe	Garigue	Total sites
Granopupa granum (Draparnaud, 1801)	1	2	4	7
Chondrina calpica calpica (Westerlund, 1872)		1		1
Cecilioides (Cecilioides) acicula (Müller, 1774)	4-4-7-	1		1
Ferussacia (Ferussacia) folliculus (Gmelin, 1790)	1	8	9	18
Rumina decollata (Linnaeus, 1758)		2	2	4
Testacella maugei Férussac, 1819			1	1
Mastus pupa (Linnaeus, 1758)	1 - 1 - 1 - 1 - 1		1	1
Oxychilus (Oxychilus) draparnaudi (Beck, 1837)		4	3	7
Oxychilus (Oxychilus) hydatinus (Rossmässler, 1854)		1		1
Parmacella (Parmacella) valencieni Webb & van Beneden, 1836		1		1
Milax gagates (Draparnaud, 1801)		2	4	6
Milax nigricans (Schluz, 1836)		3		3
Deroceras sp			1	1
Geomalacus malagensis Wiktor & Norris, 1991	1	4	1	6
Caracollina (Caracollina) lenticula (Michaud, 1831)	2	6	9	17
Gasulliella simplicula (Morelet, 1845)		1	1	2
Gittenbergeria turriplana (Morelet, 1845)			7	1
Oestophora barbula (Rossmässler, 1838)			1	1
Oestophora calpeana (Morelet, 1854)		3	2	5
Oestophora tarnieri (Morelet, 1854)			1	1
Oestophora ortizi de Winter and Ripken, 1991		1		1
Oestophora sp2			1	1
Cochlicella (Cochlicella) acuta (Müller, 1774)	14	5	4	23
Cochlicella (Cochlicella) conoidea (Draparnaud, 1801)	10		3	13
Cochlicella (Prietocella) barbara (Linnaeus, 1758)		1	2	3
Trochoidea (Trochoidea) pyradimata (Draparnaud, 1805) Trochoidea (Xerocrassa) derogata		1		1
(Rossmässler, 1854) Trochoidea (Xerocrassa) jimenensis Puente &		1		1
Arrébola, 1996			1	1
Trochoidea spl	1-1412	1		1
Trochoidea sp2		1	1	2
Trochoidea sp3			1	1
Trochoidea sp4		- A 12 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	2	2
Trochoidea sp5			1	1
Trochoidea sp6		1		1
Trochoidea sp7		1	2	3
Ponentina subvirescens (Bellamy, 1839)	1	2	13	16
Xerotrichia conspurcata (Draparnaud, 1801)	3	5	8	16
Xerotrichia apicina (Lamarck, 1822)	16	5	3	24
Candidula intersecta (Poiret, 1801)		4		4
Candidula sp1			1	1
Candidula sp2		1	Market let 5	1
Candidula sp3	1			1
Cernuella (Cernuella) virgata (Da Costa, 1778)		5	3	8
Xerosecta (Xerosecta) cespitum (Draparnaud, 1801)		1	5	6
Xerosecta (Xerosecta) promissa (Westerlund, 1893)	4	7	1	12
Xerosecta (Xerosecta) reboudiana (Bourguignat, 1863)	1	2	2	5

Species	Sand	Steppe	Garigue	Total sites
Ganula gadirana Muñoz, Almodovar & Arrébola, 1999		1		1
Iberus gualtierianus marmoratus (Férussac, 1821)	2	3	4	9
Iberus gualtierianus alonensis (Férussac, 1821)		1	M	1
Theba pisana (Müller, 1774)	18	9	12	39
Theba gittenbergeri Puente, 1994			1	1
Pseudotachea litturata (Pfeiffer, 1851)			3	3
Otala (Otala) lactea (Müller, 1774)	5	9	13	27
Eobania vermiculata (Müller, 1774)	2	1		3
Cantareus aspersus (Müller, 1774)	5	11	13	29
Number of species at each habitat type	17	39	39	

Appendix 11. The environmental variables (V) for Habitat Structure Sites. Data are totals for each of the plots individually (pa, pb, pc, pd) and total for each of the sites (all). Sites labelled S01 to S60. The variables are numbered 1 to 140 as shown below. See Table 6.5. for details.

No.	Variable
1	Soil
2	Leaf litter
3	Shingle
4	Stones
5	Rocks
6	Rubble
7	Logs
8	Other wood
9	Refuse: card/paper
10	Refuse: plastic
11	Refuse: glass
12	Refuse: other
13	Bryophytes
14	Lichen
15	Green grass 0-10cm
16	Green grass 10-20cm
17	Green grass 20-30cm
18	Green grass 30-40cm
19	Green grass 40-50cm
20	Green grass 50-60cm
21	Green grass 60-70cm
22	Green grass 70-80cm
23	Green grass 80-90cm
24	Green grass 90-100cm
25	Green grass 100-110cm
26	Green grass 110-120cm
27	Green grass 120-130cm
28	Green grass 130-140cm
29	Green grass 140-150cm
30	Green grass 150-160cm
31	Green grass 160-170cm
32	Green grass 170-180cm
33	Green grass 180-190cm
34	Green grass 190-200cm
35	Green grass >200cm
36	Dry grass 0-10cm
37	Dry grass 10-20cm
38	Dry grass 20-30cm
39	Dry grass 30-40cm
40	Dry grass 40-50cm
41	Dry grass 50-60cm
42	Dry grass 60-70cm
43	Dry grass 70-80cm
44	Dry grass 80-90cm
45	Dry grass 90-100cm
46	Dry grass 100-110cm
47	Dry grass 110-120cm
48	Dry grass 120-130cm
49	Dry grass 130-140cm
50	Dry grass 140-150cm
51	Dry grass 150-160cm
52	Dry grass 160-170cm
53	Dry grass 170-180cm

Appendix 11: The environmental variables at the Habitat Structure Sites

No.	Variable
54	Dry grass 180-190cm
55	Dry grass 190-200cm
56	Dry grass >200cm
57	Annual 0-10cm
58	Annual 10-20cm
59	Annual 20-30cm
60	Annual 30-40cm
61	Annual 40-50cm
62	Annual 50-60cm
63	Annual 60-70cm
64	Annual 70-80cm
65	Annual 80-90cm
66	Annual 90-100cm
67	Annual 100-110cm
68	Annual 110-120cm
69	Annual 120-130cm
70	Annual 130-140cm
71	Annual 140-150cm
72	Annual 150-160cm
73	Annual 160-170cm
74	Annual 170-180cm
75	Annual 180-190cm
76	Annual 190-200cm
77	Annual >200cm
78	Herb 0-10cm
79	Herb 10-20cm
80	Herb 20-30cm
81	Herb 30-40cm
82	Herb 40-50cm
83	Herb 50-60cm
84	Herb 60-70cm
85	Herb 70-80cm
86	Herb 80-90cm
87	Herb 90-100cm
88	Herb 100-110cm
89	Herb 110-120cm
90	Herb 120-130cm
91	Herb 130-140cm
92	Herb 140-150cm
93	Herb 150-160cm
94	Herb 160-170cm
95	Herb 170-180cm
96	Herb 180-190cm
97	Herb 190-200cm
98	Herb >200cm
99	Shrub 0-10cm
100	Shrub 10-20cm
101	Shrub 20-30cm
102	Shrub 30-40cm
103	Shrub 40-50cm
104	Shrub 50-60cm
105	Shrub 60-70cm
106	Shrub 70-80cm
107	Shrub 80-90cm
108	Shrub 90-100cm

Appendix 11: The environmental variables at the Habitat Structure Sites

No.	Variable
109	Shrub 100-110cm
110	Shrub 110-120cm
111	Shrub 120-130cm
112	Shrub 130-140cm
113	Shrub 140-150cm
114	Shrub 150-160cm
115	Shrub 160-170cm
116	Shrub 170-180cm
117	Shrub 180-190cm
118	Shrub 190-200cm
119	Shrub >200cm
120	Tree 0-10cm
121	Tree 10-20cm
122	Tree 20-30cm
123	Tree 30-40cm
124	Tree 40-50cm
125	Tree 50-60cm
126	Tree 60-70cm
127	Tree 70-80cm
128	Tree 80-90cm
129	Tree 90-100cm
130	Tree 100-110cm
131	Tree 110-120cm
132	Tree 120-130cm
133	Tree 130-140cm
134	Tree 140-150cm
135	Tree 150-160cm
136	Tree 160-170cm
137	Tree 170-180cm
138	Tree 180-190cm
139	Tree 190-200cm
140	Tree >200cm

Appendix 11: The environmental variables at the Habitat Structure Sites

X.I	S01	S01	S01	S01	S01	S02	S02	S02	S02	S02	S03	S03	S03	S03	S03
V	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
1	205	415	280	285	1185	185	115	250	125	675	440	360	400	117	1317
2	95	41	70	60	266	185	185	240	345	955	5	17	9	13	44
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	1	-1	0	175	0	0	180	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
13	0	0	0	5	5	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	15	0	0	15	0	0	0	0	0
15	13	5	2	13	33	5	2	0	0	7	5	9	14	27	55
16	9	5	1	9	24	0	0	0	0	0	5	4	4	5	18
17	3	0	0	2	5	0	0	0	0	0	1	2	1	3	7
18	1	0	0	2	3	0	0	0	0	0	0	1	0	1	2
19	1	0	0	2	3	0	0	0	0	0	0	0	0	1	1
20	1	0	0	2	3	0	0	0	0	0	0	0	0	1	1
21	1	0	0	1	2	0	0	0	0	0	0	0	0	1	1
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0_	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0_	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	80	17	40	125	262	4	2	4	4	14	0	1	0	11	12
37	22	5	19	112	158	3	2	4	4	13	0	1	0	0	3
38	4	1	3	58	66	1	1	2	2	3	0	0	0	0	0
39	3	0	0	41	44	1	0	0	2	3	0	0	0	0	0
40	1	0	0	31	32	1	0	0	2	3	0	0	0	0	0
41	0	0	0	11	11	1	0	0	1	1	0	0	0	0	0
42	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
43	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0,	U	U	U	0	U	0	0	0	U

Appendix 11: The environmental variables at the Habitat Structure Sites

	S01	S01	S01	S01	S01	S02	S02	S02	S02	S02	S03	S03	S03	S03	S03
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	66	13	105	27	211	130	27	9	17	183	30	21	31	21	103
58	3	1	18	13	35	2	2	6	1	11	0	1	0	0	0
59	2	1	1	1	5	0	0	1	1	2	0	0	0	0	0
60	2	0	0	0	2	0	0	0	1	1	0	0	0	0	0
61	2	0	0	0	2	0	0	0	1	1	0	0	0	0	0
62	2	0	0	0	2	0	0	0	1	1	0	0	0	0	0
63	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
64	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
65	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$\frac{0}{0}$
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76 77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	25	11	5	5	46	0	1	5	0	6	25	100	50	110	285
79	32	2	1	5	40	0	1	10	0	11	40	101	23	4	168
80	19	2	0	1	22	0	0	20	0	20	1	32	0	0	33
81	18	2	0	0	18	0	0	25	0	25	0	1	0	0	1
82	3	0	0	0	3	0	0	1	0	1	0	0	0	0	0
83	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0
84	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0
85	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0
86	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	1	0	0	0	1	0	0	0	10	10	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S01	S01	S01	S01	S01	S02	S02 pb	S02	S02	S02	S03	S03	S03	S03	S03
101	pa	pb	рс	pd	all	pa	_	pc	pd	all	pa	pb	pc	pd	all
101	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
102	25	0	0	0	25	0	0	0	0	0	0	0	0	0	0
103	25	0	0	0	25	0	0	0	0	0	0	0	0	0	0
104	30	0	0	0	30	0	0	0	0	0	0	0	0	0	0
105	10	0	0	0	10	0	0	0	0	0	0	0	0	0	0
106	10	0	0	0	10	0	0	0	0	0	0	0	0	0	0
107	10	0	0	0	10		0	0	0	0	0	0	0	0	+
108	10	0	0	0	10	0		0	0	0	0	0	0	0	0
109	10	0	0	0	10		0	0	0	0	0	0		0	0
110	10	0	0	0	10	0		0	0	0	-	0	0	0	0
111	5	0	0	0	5		0			0	0	_		-	0
112	5	0	0	0	5	0	0	0	0	0	0	0	0	0	0
113	5	0	0	0	5	0	0	0		0	0	0	-	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	-	_	0	0	0	-	-	0
116	0	0	0	0	0	0	0	0	0	0		0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0		0		+		0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0			0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	-	0	0	_	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0		0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0			0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0		0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0		0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0		0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0		0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0_	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	U	U	U	0	0	1 0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S04	S04	S04	S04	S04	S05	S05	S05	S05	S05	S06	S06	S06	S06	S06
V	pa	pb	рс	pd	all	ра	pb	рс	pd	all	pa	pb	рс	pd	all
1	450	415	150	155	1170	80	90	150	85	405	380	385	141	205	1111
2	0	0	0	17	17	8	5	5	5	23	5	9	17	26	57
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	18	0	0	0	18	0	0	0	0	0	0	0	0	0	0
5	10	0	0	0	10	1	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	7	9	156	100	272	30	22	40	80	172	8	2	26	4	40
16	1	9	1	37	48	2	2	2	0	6	2	1	12	4	19
17	1	3	0	0	4	1	0	1	0	2	1	0	2	0	3
18	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0
19	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0_	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	2	4	0	2	8	4	2	26	79	94
37	0	0	0	0	0	0	3	0	0	3	3	2	12	3	12
38	0	0	0	0	0	0	0	0	0	0	1	1	2	0	2
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0		0	0		0
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S04	S04	S04	S04	S04	S05	S05	S05	S05	S05	S06	S06	S06	S06	S06
v	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	17	75	120	220	432	395	390	315	335	1435	165	115	155	265	700
58	2	51	25	410	920	2	3	0	4	9	95	65	80	56	296
59	0	13	0	5	18	0	1	0	0_	1	5	5	4	4	18
60	0	5	0	4	9	0	0	0	0	0	1	0	0	0	1
61	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0_	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0_	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0_	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	5	67	17	89	0	0	0	0	0	0	0	0	0	0
79	0	0_	45	0	45	0	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0			0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0_	0					0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0		0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	U	U	U	0	U	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S04	S04	S04	S04	S04	S05	S05	S05	S05	S05	S06	S06	S06	S06	S06
	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	. 0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S07	S07	S07	S07	S07	S08	S08	S08	S08	S08	S09	S09	S09	S09	S09
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	230	345	90	250	915	155	470	430	55	1110	310	140	210	200	860
2	75	90	315	110	590	46	5	18	140	209	55	50	95	65	265
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	5	0	0	5	0	2	0	0	2	16	115	55	90	276
5	1	0	1	1	3	1	0	0	0	1	2	80	16	15	113
6	0	0	0	0	0	0	0	0	0	0	0	_ 0	0	0	0
7	0	0	0	0	0	0	0	1	0	1	21	0	0	5	26
8	0	0	0	0	0	0	0	0	0	0	0	5	2	0	7
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	5	5	0	0	0	0	0
11	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
13	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	58	15	35	31	139	16	9	11	8	44	9	21	17	4	51
16	2	2	3	7	14	2	1	0	2	5	4	3	3	0	10
17	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19 20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	50	21	40	60	171	13	5	0	0	18	40	30	45	35	150
37	7	3	9	48	67	5	1	0	0	6	25	17	25	17	84
38	0	1	5	5	11	2	0	0	0	2	9	5	5	2	21
39	0	1	2	3	6	1	0	0	0	1	0	0	0	0	0
40	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0		0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	U	0	U	U	U	U	U	U	U	U	0	0	0]	U	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S07	S07	S07	S07	S07	S08	S08	S08	S08	S08	S09	S09	S09	S09	S09
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	_0	0	0	0	0	0	0
57	85	28	31	55	199	22	9	13	17	51	36	35	13	13	97
58	6	1	2	40	49	23	11	7	21	62	3	1	1	0	5
59	0	0	0	10	10	1	0	1	0	2	1	0	0	0	9
60	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
61	0	0	0	1	1	0	0	0	_ 0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	_ 0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	5	0	0	0	5	250	5	36	285	576	0	25	25	80	130
79	5	0	0	0	5	40	0	16	17	73	0	60	75	150	85
80	1	0	0	0	1	7	0	0	5	12	0	65	70	160	295
81	1	0_	0	0	1	0	0	0	0	0	0	16	42	56	114
82	0	0	0	0	0	0	0	0	0	0	0	2	25	16	43
83	0	0	0	0	0	0	0	0	0	0	0	0	15	5	20
84	0	0_	0	0	0	0	0	0	0	0	0	0	1	0	1
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0_	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0_	0	0	0	0	0	0	0	0	0	0
88	0	0_	0	0	0	0_	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0_	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S07	S07	S07	S07	S07	S08	S08	S08	S08	S08	S09	S09	S09	S09	S09
	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0_	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0_	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0_	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S10	S10	S10	S10	S10	S11	S11	S11	S11	S11	S12	S12	S12	S12	S12
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	120	145	280	190	735	420	460	445	460	1785	255	190	120	155	720
2	25	30	5	21	81	13	9	9	9	40	85	85	225	125	520
3	65	65	115	80	325	0	0	0	0	0	17	25	5	17	64
4	0	0	0	0	0	0	0	0	0	0	16	26	2	15	59
5	0	0	0	0	0	0	0	0	0	0	8	1	0	6	15
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
15	3	5	5	6	19	0	0	0	0	0	1	0	8	5	14
16	1	1	1	0	3	0	0	0	0	0	0	0	4	5	9
17	0	0	0	0	0	0	0	0	0	0	0	0	4	3	7
18	0	0	0	0	0	0	. 0	0	0	0	0	0	3	3	6
19	0	0	0	0	0	0	0	0	0	0	0	0	2	3	5
20	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
21	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
22	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
23	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	75	85	95	115	370
36	0	0	0	0	0	0	0	5	1	7	21	22	70	141	254
37	0	0	0	0	0	1	0		1	2	5	5	26	93	129
38	0	0	0	0	0	0	0	1	1	2	5	3	17	17	42
39	0	0	0	0	0	0	0	0	1	1	2	2	7	4	15
40	0	0	0	0	0	0	0	0	0	1	1	1	3	3	8
41	0	0	0	0	0	0	0	0	0	0	1	0	2	1	4
42	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
43	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
44	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
45	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
46	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	U	U	U	0	0	0	1 0		0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S10	S10	S10	S10	S10	S11	S11	S11	S11	S11	S12	S12	S12	S12	S12
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	275	230	100	190	795	70	35	45	35	185	50	90	60	70	270
58	45	28	2	1	76	72	4	1	4	81	17	38	25	55	135
59	5	3	2	0	10	1	0	0	0	1	5	8	21	22	56
60	2	1	0	0	3	0	0	0	0	0	4	4	5	17	31
61	1	1	0	0	2	0	0	0	0	0	3	2	5	9	19
62	1	1	0	0	2	0	0	0	0	0	1	1	3	3	8
63	0	1	0	0	1	0	0	0	0	0	0	1	2	2	5
64	0	1	0	0	1	0	0	0	0	0	0	0	0	2	2
65	0	1	0	0	1	0	0	0	0	0	0	0	0	2	2
66	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
67	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
68	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
69	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
70	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
71	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
72	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77 78	5	27	0	15	47	0	0	0	0	0	0	0	0	0	0
79	0	7	0	5	12	0	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S10	S10	S10	S10	S10	S11	S11	S11	S11	S11	S12	S12	S12	S12	S12
101	pa	pb	рс	pd	all	pa	pb	pc	pd	all	pa	pb	pc	pd	all
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	- 0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	_ 0	0	0	0
121	0	0	0	0	0	0	0	0	0_	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	- 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S13	S13	S13	S13	S13	S14	S14	S14	S14	S14	S15	S15	S15	S15	S15
V	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	270	170	125	230	795	115	165	275	340	895	295	305	360	345	1305
2	40	45	25	40	150	100	65	66	13	244	19	18	5	5	47
3	0	0	0	0	0	95	70	55	75	295	115	60	70	60	305
4	0	0	0	0	0	25	6	16	47	94	17	35	26	21	99
5	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	55	105	105	110	375	3	2	1	1	7	0	0	0	0	0
16	5	4	4	2	15	7	2	1	1	11	0	0	0	0	0
17	0	1	1	1	3	3	2	1	1	7	0	0	0	0	0
18	0	0	0	0	0	3	1	1	1	6	0	0	0	0	0
19	0	0	0	0	0	3	1	1	0	5	0	0	0	0	0
20	0	0	0	0	0	3	1_	1	0	5	0	0	0	0	0
21	0	0	0	0	0	3	0	1	0	4	0	0	0	0	0
22	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0_	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0_	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	175	0	120	675	85	130	23	8	246	25	55	26	46	152
36	135	175	245	120	20	21	42	5	8	76	36	35	12	17	100
37	5	5	5	4	9	13	5	4	4	26	4	5	4	2	15
38	1	1		0	0	5	5	4	2	16	0	1	2	0	3
39	0	0	0	0	0	5	5	4	2	16	0	0	0	0	0
40	0	0	0	0	0	4	4	4	1	13	0	0	0	0	0
41	0	0	0	0	0	2	3	2	1	8	0	0	0	0	0
42	0	0	0	0	0	2	3	1	1	7	0	0	0	0	0
43	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	U	U	U	U	U	U	0							- 0

Appendix 11: The environmental variables at the Habitat Structure Sites

17	S13	S13	S13	S13	S13	S14	S14	S14	S14	S14	S15	S15	S15	S15	S15
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	4	9	5	5	23	81	70	85	26	262	35	26	21	25	107
58	1	1	4	1	7	50	30	26	13	119	25	17	16	4	62
59	0	0	1	0	1	62	19	14	28	123	4	5	4	2	15
60	0	0	0	0	0	62	14	18	24	118	0	3	1	1	5
61	0	0	0	0	0	37	7	17	23	84	0	1	1	0	2
62	0	0	0	0	0	23	7	6	23	59	0	1	1	0	2
63	0	0	0	0	0	2	7	5	8	22	0	0	1	0	1
64	0	0	0	0	0	0	1	5	3	9	0	0	0	0	0
65	0	0	0	0	0	0	1	5	3	9	0	0	0	0	0
66	0	0	0	0	0	0	0	1	3	4	0	0	0	0	0
67	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0
68	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0
69	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
70	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
71	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
72	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
79	0	0	0	0	0	0	0	0	0	0	5	0	0	0	5
80	0	0	0	0	0	0	0	0	0	0	5	0	0	0	5
81	0	0_	0	0	0	0	0	0	0	0	1	0	0	0	1
82	0	0	0_	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0_	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0			0		
87	0	0	0	0	0	0	0	0	0	0	0	0		0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0_	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0		0	0	0	0	0	0
96	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	5	0	0	5
100	0	0	0	0	0	0	0	U	U	U	U	1 3	0	1 0	

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S13	S13	S13	S13	S13	S14	S14	S14	S14	S14	S15	S15	S15	S15	S15
	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
101	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
102	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0_	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0_	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S16	S16	S16	S16	S16	S17	S17	S17	S17	S17	S18	S18	S18	S18	S18
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	240	161	275	415	1091	175	215	205	110	705	395	420	380	405	1600
2	100	66	96	50	312	80	115	75	125	395	30	22	40	35	127
3	25	10	1	1	37	0	30	30	20	80	0	0	0	0	0
4	15	5	3	0	23	0	11	20	2	33	0	0	0	0	0
5	1	0	0	2	3	6	1	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	5	4	1	0	10	46	21	16	35	118	0	0	0	0	0
16	5	4	1	0	10	9	3	1	9	22	0	0	, 0	0	0
17	4	1	0	0	5	1	0	0	2	3	0	0	0	0	0
18	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0_	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0_	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	620	0	0	0	0	0
36	110	55	9	9	183	165	80	100	175	520	60	16	50	25	151
37	135	25	9	2	171	105	28	62	105	300	9	6	13	5	7
38	36	4	1	0	41	5	3	4	13	25 7	0	0	2	0	2
39	8	2	1	0	11	0	0	2	4	5	0	0	0	0	0
40	1	0	0	0	1	0	0	1	2	3	0	0	0	0	0
41	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0_	0	0	0	0	0		0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	U	U	0	U	0	0	0	U

Appendix 11: The environmental variables at the Habitat Structure Sites

3.7	S16	S16	S16	S16	S16	S17	S17	S17	S17	S17	S18	S18	S18	S18	S18
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	7	41	105	31	184	30	45	70	35	180	18	35	27	31	111
58	12	16	31	9	68	13	32	13	26	84	13	18	7	7	45
59	3	4	5	3	15	0	0	3	9	12	1	11	1	1	14
60	1	1	3	2	7	0	0	3	4	7	0	2	0	1	3
61	0	1	1	0	2	0	0	3	2	5	0	1	0	1	2
62	0	0	0	0	0	0	0	2	2	4	0	1	0	0	1
63	0	0	0	0	0	0	0	1	1	2	0	1	0	0	1
64	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85 86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	U	U	0	0					4-11-2					1916	

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S16 pa	S16 pb	S16 pc	S16 pd	S16 all	S17 pa	S17 pb	S17 pc	S17 pd	S17 all	S18 pa	S18 pb	S18 pc	S18 pd	S18 all
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0_	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S19	S19	S19	S19	S19	S20	S20	S20	S20	S20	S21	S21	S21	S21	S21
V	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	400	350	355	355	1460	285	325	390	320	1320	120	71	55	70	316
2	27	60	36	45	168	65	65	36	56	222	120	9	40	18	187
3	10	17	6	45	78	0	6	0	0	6	1	50	22	17	90
4	0	0	0	0	0	0	0	0	0	0	10	80	60	110	260
5	0	0	0	0	0	1	0	0	0	1	110	220	195	250	775
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
15	0	0	0	0	0	9	3	0	0	12	0	0	0	0	0
16	0	0	0	0	0	5	3	0	0	8	0	0	0	0	0
17	0	0	0	0	0	5	3	0	0	8	0	0	0	0	0
18	0	0	0	0	0	5	3	0	0	8	0	0	0	0	0
19	0	0	0	0	0	4	2	0	0	6	0	0	0	_ 0	0
20	0	0	0	0	0	2	1	0	0	3	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	36	25	45	21	127	140	100	55	91	486	85	65	80	31	261
37	16	16	31	11	74	90	50	27	32	199	76	46	125	13	260
38	3	2	9	2	16	46	13	9	8	76	76	24	52	5	157
39	1	1	5	2	9	21	3	1	3	28	62	9	22	5	98
40	0	0	1	1	2	12	2	0	0	14	57	9	9	5	80
41	0	0	0	0	0	2	0	0	0	2	17	5	5	3	30
42	0	0	0	0	0	0	0	0	0	0	17	3	5	0	25
43	0	0	0	0	0	0	0	0	0	0	16	3	5	0	24
44	0	0	0	0	0	0	0	0	0	0	3	2	2	0	7
45	0	0	0	0	0	0	0	0	0	0	2	0	2	0	4
46	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
47	0	0	0	0	0	0	0	0_	0	0	1	0	0	0	1
48	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
49	0	0	0	0	0	0	0	0_	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S19	S19	S19	S19	S19	S20	S20	S20	S20	S20	S21	S21	S21	S21	S21
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	31	51	60	35	177	7	8	22	36	73	25	3	4	5	37
58	40	31	35	18	124	12	3	12	25	53	23	3	3	5	34
59	30	18	17	12	77	7	2	7	4	20	22	1	2	4	29
60	7	8	4	2	21	7	2	2	1	12	22	0	2	2	26
61	1	1	1	1	4	1	0	0	0	1	7	0	2	0	9
62	0	0	0	0	0	0	0	0	0	0	6	0	1	0	7
63	0	0	0	0	0	0	0	0	0	0	5	0	1	0	6
64	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
65	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
66	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
67	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
68	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	25	5	6	7	43
79	0	0	0	0	0	0	0	0	0	0	50	5	10	25	90
80	0	0	0	0	0	0	0	0	0	0	65	5	10	12	92
81	0	0	0	0	0	0	0	0	0	0	65	5	6	3	88
82	0	0	0	0	0	0	0	0	0	0	65	5	2	2	75
83	0	0	0	0	0	0	0	0	0	0	50	5	2	0	57
84	0	0	0	0	0	0	0	0	0	0	45	0	1	0	46
85	0	0	0_	0	0	0	0	0	0	0	11	0	0	0	11
86	0	0	0	0	0	0	0	0	0	0	7	0	0	0	7
87	0	0	0	0	0	0	0	0	0	0	6	0	0	0	6
88	0	0	0	0	0	0	0	0	0	0	6	0	0	0	6
89	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
90	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
91	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0		0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0		0	0
98	0	0	0	0	0	0	0	0	0	0	10	5	15	0	0
100	0	0	0	0	0	0	0	0	U	0	10	3	13	U	30

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S19	S19	S19	S19	S19	S20	S20	S20	S20	S20	S21	S21	S21	S21	S21
	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	0	0	0	0	0	0	0	0	0	0	20	5	40	0	65
102	0	0	0	0	0	0	0	0	0	0	30	5	40	0	75
103	0	0	0	0	0	0	0	0	0	0	35	5	45	0	85
104	0	0	0	0	0	0	0	0	0	0	35	5	40	0	80
105	0	0	0	0	0	0	0	0	0	0	40	5	10	0	55
106	0	0	0	0	0	0	0	0	0	0	50	1	10	0	61
107	0	0	0	0	0	0	0	0	0	0	55	0	10	0	65
108	0	0	0	0	0	0	0	0	0	0	55	0	5	0	60
109	0	0	0	0	0	0	0	0	0	0	55	0	1	0	56
110	0	0	0	0	0	0	0	0	0	0	55	0	1	0	56
111	0	0	0	0	0	0	0	0	0	0	55	0	0	0	55
112	0	0	0	0	0	0	0	0	0	0	55	0	0	0	55
113	0	0	0	0	0	0	0	0	0	0	55	0	0	0	55
114	0	0	0	0	0	0	0	0	0	0	55	0	0	0	55
115	0	0	0	0	0	0	0	0	0	0	55	0	0	0	55
116	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
117	0	0	0	0	0	0	0	0	0	0	5	0	0	0	5
118	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	10	0	10
130	0	0	0	0	0	0	0	0	0	0	0	0	10	0	10
131	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5
132	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

FAU	S22	S22	S22	S22	S22	S23	S23	S23	S23	S23	S24	S24	S24	S24	S24
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	195	95	80	130	500	195	160	275	225	855	31	36	17	6	90
2	130	17	46	55	248	9	13	5	18	45	13	13	8	5	39
3	0	5	0	5	10	85	80	75	50	290	90	95	115	215	515
4	15	11	3	0	29	100	80	50	41	271	85	60	125	145	415
5	42	46	30	6	124	90	130	35	60	315	76	85	185	100	446
6	0	1	12	1	14	0	0	0	0	0	0	0	0	0	0
7	0	0	1	0	1	1	0	1	0	2	0	1	0	10	11
8	0	0	25	0	25	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	1	0	2	0	3	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0
13	51	15	1	0	67	5	1	2	7	15	55	40	7	0	106
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	8	50	80	35	173	5	18	21	4	45	106	70	21	13	210
16	3	76	3	3	85	0	2	3	0_	5	0	9	12	4	25
17	1	2	2	3	8	0	1	0	0	1	0	0	5	4	9
18	1	0	0	0	1	0	1	0	0	1	0	0	4	3	7
19	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
20	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0				0	0	0	0	0	0	0
35	0	0	0	0	0	5	9	13	5	32	9	32	5	5	51
36	4	10	35	15	12	0	0	0	3	52	3	32	5	5	45
37	4	1	5	2	2	0	0	0	2	. 9	3	14	5	4	26
38	0	0	1	0	0	0	0	0	1	2	2	7	5	3	17
39	0	0	0	0	0	0	0	0	0	0	2	1	2	2	7
40	0	0	0	0	0	0	0	0	0	0	2	0	0	1	3
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	U	U			0	0							

Appendix 11: The environmental variables at the Habitat Structure Sites

	S22	S22	S22	S22	S22	S23	S23	S23	S23	S23	S24	S24	S24	S24	S24
V	pa	pb	pc	pd	all	pa	pb	pc	pd	all	pa	pb	pc	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	70	235	200	260	765	5	18	21	101	154	41	70	21	25	157
58	45	211	2	1	259	4	2	3	3	20	1	1	5	27	34
59	40	0	0	0	40	4	1	0	1	27	0	0	4	9	13
60	40	0	0	0	40	2	1	0	1	8	0	0	3	4	7
61	40	0	0	0	40	2	0	0	0	6	0	0	1	4	5
62	35	0	0	0	35	0	0	0	0	0	0	0	0	2	2
63	31	0	0	0	31	0	0	0	0	0	0	0	0	2	2
64	20	0	0	0	20_	0	0	0	0	0	0	0	0	0	0
65	20	0	0	0	20	0	0	0	0	0	0	0	0	0	0
66	7	0	0	0	7	0	0	0	0	0	0	0	0	0	0
67	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	1	1	2	2	0	0	4
78 79	0	0	0	0	0	0	0	0	5	5	10	10	0	0	20
80	0	0	0	0	0	0	0	0	10	10	10	6	0	0	16
81	0	0	0	0	0	0	0	0	10	10	5	1	0	0	6
82	0	0	0	0	0	0	0	0	10	10	1	0	0	0	1
83	0	0	0	0	0	0	0	0	5	5	0	0	0	0	0
84	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	8	8	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S22	S22	S22	S22	S22	S23	S23	S23	S23	S23	S24	S24	S24	S24	S24
v	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	0	0	0	0	0	0	0	0	12	12	0	0	0	0	0
102	0	0	0	0	0	0	0	0	11	11	0	0	0	0	0
103	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0
104	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0
105	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	- 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S25	S25	S25	S25	S25	S26	S26	S26	S26	S26	S27	S27	S27	S27	S27
V	pa	pb	pc	pd	all	pa	pb	pc pc	pd	all	pa	pb	pc pc	pd	all
1	27	23	17	5	72	17	9	26	85	137	105	85	120	115	425
2	5	5	13	5	28	17	21	26	22	86	5	13	9	5	32
3	35	80	200	140	455	55	26	41	80	202	0	0	5	0	5
4	75	190	85	60	410	100	36	95	80	311	0	0	2	1	3
5	290	155	61	75	581	22	55	21	55	153	20	11	1	56	88
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	1	0	2	3	0	0	0	0	0
8	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	17	9	14	5	45	160	95	150	120	525	75	130	50	80	335
16	35	13	14	9	71	8	5	3	9	25	26	24	9	13	72
17	14	2	7	3	26	2	3	2	4	- 11	9	3	3	5	20
18	7	1	5	3	16	1	1	1	3	6	5	1	1	3	10
19	6	0	1	1	8	0	0	0	2	2	5	1	1	1	8
20	1	0	1	0	1	0	0	0	2	2	3	1	0	0	4
21	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
22	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0_	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0_	0	0	31	26	74	12	12	5	9	38
36	18	1	1	0	20	5	12	0	3	3	0	0	0	0	0
37	28	1	1	0	30	0	0	0	1	1	0	0	0	0	0
38	2	0	1	0	3	0	0	0	1	1	0	0	0	0	0
39	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
40	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
41	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47		_	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
_			0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0]	U	U	0	0							

Appendix 11: The environmental variables at the Habitat Structure Sites

1.7	S25	S25	S25	S25	S25	S26	S26	S26	S26	S26	S27	S27	S27	S27	S27
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	45	50	120	205	420	131	205	115	40	491	300	240	315	245	1101
58	195	1	105	281	582	8	17	9	6	40	190	28	42	27	287
59	170	0	17	28	215	1	4	1	0	6	75	38	20	11	144
60	6	0	6	5	17	0	1	0	0	1	48	20	7	2	77
61	2	0	5	1	8	0	0	0	0	0	21	5	6	1	33
62	0	0	1	0	1	0	0	0	0	0	1	1	6	0	8
63	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75 76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S25	S25	S25	S25	S25	S26	S26	S26	S26	S26	S27	S27	S27	S27	S27
	pa	pb	pc	pd	all	pa	pb	pc	pd	all	pa	pb	рс	pd	all
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S28	S28	S28	S28	S28	S29	S29	S29	S29	S29	S30	S30	S30	S30	S30
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	50	120	95	290	555	65	75	40	35	215	40	35	45	35	155
2	35	40	30	36	141	25	30	40	25	120	45	50	40	95	230
3	0	0	21	13	34	55	55	75	55	240	13	26	30	14	83
4	0	0	35	16	51	55	130	105	65	355	86	55	65	8	214
5	0	0	80	1	81	60	10	11	46	127	131	165	81	4	381
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2
8	0	0	0	0	0	0	1	0	2	3	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
10	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	5	0	0	0	5	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	70	70	140	25	245	150	60	85	36	331	100	60	50	9	219
16	70	85	165	26	242	225	85	110	37	455	131	57	25	9	222
17	36	75	106	14	151	50	57	25	8	140	17	5	2	1	25
18	31	26	32	7	49	7	13	5	5	30	2	1	0	0	3
19	26	8	12	1	36	1	4	2	1	8	0	0	0	0	0
20	11	3	6	0	16	0	0	0	1	1	0	0	0	0	0
21	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0
22	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	- 0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0_	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0_	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
36	320	250	140	105	815	55	30	40	9	134	26	18	9 5	2	56
37	270_	45	165	86	766	70	17	30	14	39	14	12	1	2	33
38	236	215	106	18	569	17	5	9	8	18	2	0	0	1	3
39	207	135	32	7	379	4	4	5	1	14	1	0	0	0	1
40	86	47	12	1	89	4	4		1	11	0	0	0	0	0
41	40	9	6	1	204	2	4	3	1	6	0	0	0	0	0
42	3	3	2	0	0	0	2		1	3	0	0	0	0	0
43	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0
44	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	U	0	U	U		0	1 0	

Appendix 11: The environmental variables at the Habitat Structure Sites

	S28	S28	S28	S28	S28	S29	S29	S29	S29	S29	S30	S30	S30	S30	S30
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	26	22	21	25	94	32	10	110	235	487	35	50	140	12	237
58	8	17	13	5	43	52	220	155	335	762	41	66	145	16	268
59	4	8	9	4	25	15	130	55	35	235	13	11	9	1	34
60	4	2	3	1	10	3	26	12	5	46	1	1	2	1	5
61	3	2	1	0	6	0	8	9	1	18	0	1	1	1	3
62	1	1	1	0	3	0	4	3	0	18	0	1	0	1	2
63	1	0	0	0	1	0	4	3	0	7	0	0	0	0	0
64	1	0	0	0	0	0	4	3	0	7	0	0	0	0	0
65	0	0	0	0	0	0	4	3	0	7	0	0	0	0	0
66	0	0	0	0	0	0	4		0	7	0	0	_	+	0
67	0	0	0	0	0	0	4	3	0	7	0	0	0	0	0
68	0	0	0	0	0	0	4	3	0	7	0	0	0	0	0
69	0	0	0	0	0	0	3	3	0	6	0	0	0	0	0
70	0	0	0	0	0	0	2	2	0	4	0	0	0	0	0
72	0	0	0	0	0	0	2	2	0	4	0	0	0	0	0
73	0	0	0	0	0	0	2	2	0	4	0	0	0	0	0
74	0	0	0	0	0	0	2	1	0	3	0	0	0	0	0
75	0	0	0	0	0	0	2	1	0	3	0	0	0	0	0
76	0	0	0	0	0	0	2	1	0	3	0	0	0	0	0
77	0	0	0	0	0	0	2	1	0	3	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	30	40	51	300	421
79	0	0	0	0	0	0	0	0	0	0	35	50	60	385	530
80	0	0	0	0	0	0	0	0	0	0	7	1	4	9	21
81	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0_	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	U	0		0	0	0	U	1 0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S28	S28	S28	S28	S28	S29	S29	S29	S29	S29	S30	S30	S30	S30	S30
	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	- 0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0_	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0_	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S31	S31	S31	S31	S31	S32	S32	S32	S32	S32	S33	S33	S33	S33	S33
V		pb	pc	pd	all	pa	pb	pc pc	pd	all	pa	pb	pc	pd	all
1	140	146	96	37	419	25	45	50	50	170	95	5	8	2	110
2	50	36	80	95	261	80	40	40	40	220	60	105	95	240	500
3	60	50	150	130	390	0	0	0	0	0	170	60	28	12	565
4	40	75	85	75	275	1	0	1	1	3	125	140	50	45	360
5	85	86	40	140	351	60	36	41	80	217	32	125	305	180	642
6	0	0	0	0	0	0	0	0	0	0	0	2	8	3	13
7	7	3	2	1	13	0	0	0	1	1	3	2	0	1	6
8	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	4	1	0	0	5
12	0	0	0	0	0	0	0	0	0	0	1	1	2	2	6
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	2	5	5	16	28	0	0	0	0	0
15	0	0	0	0	0	5	4	2	4	15	0	0	0	0	0
16	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0_	0	0	0	0	0	0	0	0	0	0	0
36	30	0	22	11	63	315	305	360	300	1280	25	36	10	15	86
37	25	0_	12	1	38	23	8	9	9	49	20	41	10	10	81
38	2	0	3	1	6	5	4	3	5	17	20	41	11	5	77
39	0	0	0	0	0	2	3	3	5	13	20	31	6	5	62
40	0	0	0	0	0	2	3	1	3	9	20	21	6	1	48
41	0	0	0	0	0	1	1	1	1	4	16	6	2	1	25
42	0	0	0	0	0	0	0	0	1	1	11	2	1	1	15
43	0	0	0	0	0	0_	0	0	0	0	6	2	1	1	10
44	0	0	0	0	0	0	0	0	0	0	6	2	0	0	8
45	0	0	0	0	0	0	0	0	0	0	1	2	0	0	3
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S31	S31	S31	S31	S31	S32	S32	S32	S32	S32	S33	S33	S33	S33	S33
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	57	102	18	22	199	8	5	1	2	16	5	13	4	2	24
58	58	73	9	18	158	2	1	0	0	3	4	9	4	2	19
59	4	24	2	4	34	0	0	0	0	0	2	9	4	2	17
60	3	5	0	3	11	0	0	0	0	0	2	4	4	2	12
61	3	4	0	3	10	0	0	0	0	0	1	4	4	2	11
62	2	3	0	3	8	0	0	0	0	0	1	4	4	2	11
63	2	3	0	3	8	0	0	0	0	0	1	4	4	2	11
64	2	2	0	2	6	0	0	0	0	0	1	4	3	2	10
65	2	1	0	2	5	0	0	0	0	0	1	3	3	2	10
66	0	1	0	0	1	0	0	0	0	0	1	2	2	2	7
67	0	1	0	0	1	0	0	0	0	0	1	2	1	2	6
68	0	0	0	0	0	0	0	0	0	0	0	0	1	6	6
69	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0_	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	17	26	17	21	81	0	0	1	1	2
78	0	0	0	0	0	45	61	50	61	217	0	0	1	1	2
79	0	0	0	0	0	32	25	18	15	90	0	0	1	1	2
80	0	0	0	0	0	3	1	2	1	7	0	0	1	1	2
81	0	0	0	0	0	1	1	0	0	2	0	0	1	1	2
82	0	0	0	0	0	0	1	0	0	1	0	0	1	1	2
$\overline{}$		0	0	0	0	0	0	0	0	0	0	0	1	1	2
84	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	2	2	1	30	0	1	32	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S31	S31	S31	S31	S31	S32	S32	S32	S32	S32	S33	S33	S33	S33	S33
	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	0	0	0	15	15	1	55	0	1	57	0	0	0	0	0
102	0	0	0	15	15	0	60	0	0	60	0	0	0	0	0
103	0	0	0	15	15	0	1	0	0	1	0	0	0	0	0
104	0	0	0	20	20	0	0	0	0	0	0	0	0	1	1
105	0	0	0	20	20	0	0	0	0	0	0	0	0	5	5
106	0	0	0	15	15	0	0	0	0	0	0	0	0	5	5
107	0	0	0	15	15	0	0	0	0	0	0	0	0	5	5
108	0	0	0	15	15	0	0	0	0	0	0	0	0	5	5
109	0	0	0	10	10	0	0	0	0	0	0	0	0	5	5
110	0	0	0	10	10	0	0	0	0	0	0	0	0	5	5
111	0	0	0	5	5	0	0	0	0	0	0	0	0	5	5
112	0	0	0	5	5	0	0	0	0	0	0	0	0	5	5
113	0	0	0	5	5	0	0	0	0	0	0	0	0	5	5
114	0	0	0	5	5	0	0	0	0	0	0	0	0	5	5
115	0	0	0	1	1	0	0	0	0	0	0	0	0	5	5
116	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
117	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
118	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
119	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0_	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
128	0	5	0	0	5	0	0	0	0	0	0	0	0	0	0
129	0	15	0	1	16	0	0	0	0	0	0	0	0	0	0
130	0	45	0	5	50	0	0	0	0	0	0	0	0	0	0
131	0	45	0	5	50	0	0	0	0	0	0	0	0	0	0
132	0	45	5	10	60	0	0	0	0	0	0	0	0	0	0
133	0	45	6	20	71	0	0	0	0	0	0	0	0	0	0
134	0	45	11	30	86	0	0	0	0	0	0	0	0	0	0
135	0	45	11	40	96	0	0	0	0	0	0	0	0	0	0
136	0	45	10	80	135	0	0	0	0	0	0	0	0	0	0
137	0	45	10	85	140	0	0	0	0	0	0	0	0	0	0
138	0	45	20	85	150	0	0	0	0	0	0	0	0	0	0
139	0	50	90	90	230	0	0	0	0	0	0	0	0	0	0
140	0	50	90	90	230	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S34	S34	S34	S34	S34	S35	S35	S35	S35	S35	S36	S36	S36	S36	S36
V	pa	pb	pc	pd	all	pa	pb	pc	pd	all	pa	pb	pc	pd	all
1	205	60	50	320	635	45	205	106	65	421	25	30	100	30	180
2	60	21	55	13	149	40	30	36	13	119	13	25	9	25	72
3	11	0	1	6	18	50	30	120	115	315	55	45	110	35	145
4	3	9	1	17	30	80	55	85	140	360	65	80	170	60	375
5	1	0	6	1	9	145	120	120	207	592	4	26	31	13	74
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	2	1	3	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	2	0	1	3	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	10	10	0	1	32	8	41
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	5	0	0	0	5	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	150	350	260	140	900	31	16	17	32	96	335	285	46	315	981
37	13	190	31	9	243	9	22	18	27	76	5	21	13	17	103
38	3	13	13	4	33	4	4	3	4	10	5	5	3	5	18
39	2	5	4	1	12	2	3	1	4	9	5	5	3	5	18
40	2	4	4	0	10	2	2	1	2	5	5	5	2	5	17
41	2	3	3	0	8	1	1	1	1	4	4	5	2	5	16
42	0	0	1	0	1	1	0	0	0	1	4	5	2	5	16
43	0	0	1	0	1	1	0	0	0	1	2	3	2	5	12
44	0	0	1	0	1	1	0	0	0	1	1	3	0	2	6
45	0	0	0	0	0	0	0	0	0	0	0	1	0	2	3
46	0	0	0	0	0		0	0	0	0	0	0	0	1	1
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	U	U	U	U	0						

Appendix 11: The environmental variables at the Habitat Structure Sites

**	S34	S34	S34	S34	S34	S35	S35	S35	S35	S35	S36	S36	S36	S36	S36
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	70	70	120	8	268	115	46	21	9	191	9	5	5	5	24
58	13	17	33	3	66	90	56	41	18	205	2	1	1	3	7
59	7	5	4	0	16	2	17	4	8	31	2	0	0	2	4
60	2	3	2	0	7	1	4	3	1	9	0	0	0	1	1
61	0	2	2	0	3	1	2	2	1	6	0	0	0	0	0
62	0	0	1	0	1	1	2	0	1	4	0	0	0	0	0
63	0	0	0	0	0	1	2	0	1	4	0	0	0	0	0
64	0	0	0	0	0	1	2	0	0	3	0	0	0	0	0
65	0	0	0	0	0	0	2	0	5	7	0	0	0	0	0
66	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
67	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
68	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
69	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
70	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
71	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
72	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
73	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
74	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
75	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
76 77	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0
78	0	0	0	0	0	0	1	0	0	1	0	13	13	25	51
79	0	0	0	0	0	0	5	0	0	5	0	21	17	45	83
80	0	0	0	0	0	0	1	0	0	1	0	17	4	32	53
81	0	0	0	0	0	0	1	0	0	1	0	5	3	13	21
82	0	0	0	0	0	0	0	0	0	0	0	3	1	7	11
83	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S34	S34	S34	S34	S34 all	S35	S35	S35	S35	S35	S36	S36	S36	S36	S36
101	pa	pb	рс	pd		pa	pb	рс	pd	all	pa	pb	pc	pd	all
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	0			0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	. 0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

G U T	S37	S37	S37	S37	S37	S38	S38	S38	S38	S38	S39	S39	S39	S39	S39
V	pa	pb	pc	pd	all	pa	pb	pc	pd	all	pa	pb	pc	pd	all
1	55	180	55	45	335	280	105	356	285	1035	80	60	225	50	400
2	85	55	75	130	345	140	60	43	100	343	50	40	26	35	151
3	0	10	0	0	10	13	9	25	25	72	0	0	0	0	0
4	0	16	0	1	17	0	1	5	8	14	1	11	0	0	12
5	2	20	2	5	29	0	0	0	0	0	1	31	26	0	58
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	1	0	0	0	1	0	0	0	0	0	2	0	5	25	32
8	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	15	15	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	5	210	13	3	33	1	2	13	11	27	17	30	5	17	69
16	7	12	8	1	22	1	2	8	6	17	17	17	5	5	44
17	1	4	0	1	3	0	2	2	1	5	4	5	3	1	13
18	0	1	0	0	0	0	0	2	0	2	3	1	0	0	4
19	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1
20	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0_	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	27	356	325	310	195	365	1195
36	335	210	355	285	1185	17	280	32		147	315	165	95	300	875
37	67	12	27	131	237	8	85	36	18	21	313	33	38	165	266
38	7	4	3	9	23	5	8	3	4	40	13	5	9	30	57
39	2	1	2	3	8	1	32	3	2	10	13	2	3	5	23
40	2	1	0	1	4	1	4	2	1	8	4	0	3	5	12
41	1	1	0	1	3	1	3	2	0	6	4	0	3	5	12
42	0	0	0	0	0	1	2	2	0	5	4	0	1	3	8
43	0	0	0	0	0		2	2	0	5	3	0	1	3	7
44	0	0	0	0	0	1	2	0	0	3	3	0	1	2	6
45	0	0	0	0	0	1	0	0	0	1	3	0	0	1	4
46	0	0	0	0	0		0	0	0	0	2	0	0	1	3
47	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
48	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	U	0	0	0_	0		0			0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S37	S37	S37	S37	S37	S38	S38	S38	S38	S38	S39	S39	S39	S39	S39
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	26	5	9	16	56	55	40	26	55	176	30	21	26	13	90
58	41	12	13	16	82	100	70	26	51	247	35	27	30	13	105
59	22	1	4	3	30	200	75	17	37	329	40	5	17	5	67
60	1	0	1	2	4	210	75	16	31	332	35	8	9	5	57
61	0	0	0	0	0	220	70	15	16	321	26	11	4	4	45
62	0	0	0	0	0	205	60	10	15	290	26	11	4	2	43
63	0	0	0	0	0	171	46	10	11	238	17	11	1	2	31
64	0	0	0	0	0	81	45	10	11	147	15	11	0	2	28
65	0	0	0	0	0	66	26	10	5	107	15	10	0	0	25
66	0	0	0	0	0	56	11	10	1	78	15	10	0	0	25
67	0	0	0	0	0	8	3	1	1	13	15	2	0	0	17
68	0	0	0	0	0	2	0	0	1	3	5	2	0	0	7
69	0	0	0	0	0	2	0	0	1	3	6	1	0	0	7
70	0	0	0	0	0	2	0	0	1	3	0	0	0	0	0
71	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0
72	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
73 74	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
75	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
76	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
77	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	5	5	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S37	S37	S37	S37	S37	S38	S38	S38	S38	S38	S39	S39	S39	S39	S39
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	0	0	0	40	40	0	0	0	0	0	0	0	0	0	0
102	0	0	0	50	50	0	0	0	0	0	0	0	0	0	0
103	0	0	0	50	50	0	0	0	0	0	0	0	0	0	0
104	0	0	0	50	50	0	0	0	0	0	0	0	0	0	0
105	0	0	0	30	30	0	0	0	0	0	0	0	0	0	0
106	0	0	0	20	20	0	0	0	0	0	0	0	0	0	0
107	0	0	0	20	20	0	0	0	0	0	0	0	0	0	0
108	0	0	0	20	20	0	0	0	0	0	0	0	0	0	0
109	0	0	0	5	5	0	0	0	0	0	0	0	0	0	0
110	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	. 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0_	0	0	0	0	0	1 0	1 0	1 0	1 0

Appendix 11: The environmental variables at the Habitat Structure Sites

2.315.6	S40	S40	S40	S40	S40	S41	S41	S41	S41	641	642	642	642	642	C42
V		pb		pd pd	all	pa pa	pb	-27-17	pd pd	S41 all	S42 pa	S42 pb	S42	S42 pd	S42 all
1	985	100	pc 145	105	435	65	85	pc 230	71	451	115	66	90	40	311
2	50	40	35	45	170	60	120	115	81	376	50	81	240	175	546
3	17	25	45	30	117	2	0	17	16	35	0	0	0	0	0
4	12	45	50	9	116	5	0	10	0	15	0	0	0	0	0
5	2	6	1	1	10	66	5	20	0	91	40	225	27	195	487
6	0	0	0	0	0	0	25	1	186	212	0	0	0	0	0
7	0	0	0	0	0	0	1	1	0	2	1	0	0	0	1
8	0	0	0	0	0	0	5	0	0	5	0	0	1	0	1
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	1	0	6	7	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	25	25	15	15	80	2	1	1	6	10
14	0	0	0	0	0	25	0	0	0	25	1	12	0	0	13
15	3	0	8	1	12	4	5	1	2	12	17	7	1	2	27
16	3	0	1	0	4	4	5	1	2	12	13	7	1	2	23
17	0	0	0	0	0	3	4	1	1	9	5	3	0	1	9
18	0	0	0	0	0	1	3	1	1	6	3	2	0	0	5
19	0	0	0	0	0	1	1	1	0	3	2	2	0	0	4
20	0	0	0	0	0	0	1	1	0	2	2	1	0	0	3
21	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	330	160	195	245	930	210	220	55	75	560	26	21	11	16	74
37	195	46	71	87	399	240	195	60	105	600	33	7	7	8	55
38	120	13	32	28	193	115	55	45	87	302	18	3	0	1	22
39	70	8	8	17	103	46	31	23	33	133	8	2	0	1	11
40	17	4	4	12	37	13	9	14	13	49	6	2	0	1	9
41	13	2	3	7	25	5	8	9	7	29	2	1	0	0	3
42	13	0	2	7	22	5	3	9	3	20	1	0	0	0	1
43	5	0	0	7	12	3	1	4	2	10	1	0	0	0	1
44	5	0	0	2	7	2	0	3	2	7	0	0	0	0	0
45	5	0	0	1	6	1	0	3	1	5	0	0	0	0	0
46	2	0	0	0	2	0	0	1	0	1	0	0	0	0	0
47	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

17	S40	S40	S40	S40	S40	S41	S41	S41	S41	S41	S42	S42	S42	S42	S42
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	13	43	37	40	133	0	17	8	3	28	5	5	12	8	30
58	18	9	13	5	45	0	9	7	3	19	5	4	8	23	40
59	17	3	8	2	30	0	4	12	3	19	4	2	3	6	15
60	15	1	2	0	18	0	4	7	3	14	2	1	1	6	10
61	5	0	0	0	5	0	4	3	1	8	2	1	1	6	10
62	5	0	0	0	5	0	3	2	0	5	2	0	1	6	9
63	1	0	0	0	1	0	3	2	0	5	1	0	1	1	3
64	0	0	0	0	0	0	2	1	0	3	1	0	1	0	2
65	0	0	0	0	0	0	1	1	0	2	1	0	1	0	2
66	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
67	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70 71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	60	10	27	35	132	205	61	120	50	436
79	0	0	0	0	0	125	15	22	60	222	275	100	195	105	675
80	0	0	0	0	0	150	25	81	60	316	245	96	215	100	656
81	0	0	0	0	0	170	30	80	70	350	240	71	200	101	612
82	0	0	0	0	0	175	30	85	65	355	225	75	175	100	575
83	0	0	0	0	0	165	30	72	61	328	235	36	146	71	488
84	0	0	0	0	0	155	30	72	42	299	101	1	102	35	238
85	0	0	0	0	0	80	30	57	21	188	60	0	95	5	160
86	0	0	0	0	0	41	10	41	11	103	51	0	1	0	52
87	0	0	0	0	0	12	5	10	5	32	50	0	0	0	50
88	0	0	0	0	0	6	0	2	1	9	1	0	0	0	1
89	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	56	46	0	16	118
100	0	0	0	0	0	0	0	0	0	U	30	40	1 0	10	118

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S40	S40	S40	S40	S40	S41	S41	S41	S41	S41	S42	S42	S42	S42	S42
1.0.1	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	0	0	0	0	0	0	0	0	0	0	135	76	0	26	237
102	0	0	0	0	0	0	0	0	0	0	95	41	0	25	161
103	0	0	0	0	0	0	0	0	0	0	90	35	0	16	141
104	0	0	0	0	0	0	0	0	0	0	67	25	0	5	97
105	0	0	0	0	0	0	0	0	0	0	35	6	0	0	41
106	0	0	0	0	0	0	0	0	0	0	30	1	0	0	31
107	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
108	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
109	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

* 7	S43	S43	S43	S43	S43	S44	S44	S44	S44	S44	S45	S45	S45	S45	S45
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	180	180	165	160	685	180	90	75	120	465	75	50	65	80	270
2	80	115	115	95	405	85	85	50	95	315	140	70	135	130	475
3	5	0	0	0	5	15	50	30	10	105	0	0	0	0	0
4	5	0	0	0	5	30	85	50	6	161	0	0	0	0	0
5	15	0	80	22	117	0	21	0	25	46	22	8	3	0	33
6	0	0	0	0	0	36	0	0	2	38	_ 0	0	0	0	0
7	0	0	2	10	0	1	0	5	0	6	0	0	0	0	0
8	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	1	0	0	2	3	0	0	0	0	0
11	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	35	16	17	21	89	30	40	150	75	295	40	30	55	65	190
14	0	0	0	0	0	0	0	0	0	0	5	0	0	0	5
15	31	55	40	70	196	55	65	80	95	295	25	60	45	45	175
16	27	70	56	60	213	280	140	140	125	685	27	37	22	28	114
17	3	3	9	3	18	290	165	150	145	750	5	28	8	9	50
18	2	1	2	1	6	290	170	125	145	730	3	18	4	4	29
19	0	0	2	0	2	220	120	75	115	530	0	2	2	2	6
20	0	0	1	0	1	140	72	37	75	324	0	0	0	0	0
21	0	0	1	0	1	51	60	21	70	202	0	0	0	0	0
22	0	0	0	0	0	21	26	11	32	90	0	0	0	0	0
23	0	0	0	0	0	16	6	1	6	29	0	0	0	0	0
24	0	0	0	0	0	2	5	0	2	9	0	0	0	0	0
25	0	0	0	0	0	0	1	0	1	2	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0		0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	31	40	30	65	166	45	45	55	55	200	25	22	25	35	107
37	32	105	32	55	224	115	70	70	70	325	13	5	5	14	37
38	8	3	5	33	19	100	80	70	65	315	5	5	5	9	24
39	3	2	5	1	11	90	75	60	65	290	3	2	3	3	11
40	0	1	4	0	5	90	40	40	60	230	1	2	0	1	4
41	0	1	3	0	4	32	32	26	45	135	0	0	0	0	0
41	0	0	3	0	3	17	22	13	40	92	0	0	0	0	0
43	0	0	0	0	0	12	7	7	36	62	0	0	0	0	0
44	0	0	0	0	0	7	2	1	13	23	0	0	0	0	0
45	0	0	0	0	0	2	0	0	12	14	0	0	0	0	0
46	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	-	U	U	U											74 QL S.

Appendix 11: The environmental variables at the Habitat Structure Sites

	S43	S43	S43	S43	S43	S44	S44	S44	S44	S44	S45	S45	S45	S45	S45
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	55	31	21	46	153	13	12	5	5	25	50	85	45	65	245
58	26	18	26	42	55	26	22	8	3	59	8	2	2	4	16
59	13	1	8	3	25	8	2	2	1	13	2	2	2	4	10
60	6	1	5	0	12	1	0	1	0	2	1	1	2	3	7
61	5	0	1	0	6	0	0	0	0	0	1	1	2	3	7
62	1	0	0	0	1	0	0	0	0	0	0	1	1	3	5
63	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	5	0	9	0	13	20	12	5	15	54	35	21	25	3	84
79	5	0	13	0	18	30	27	17	25	99	51	26	41	11	129
80	5	0	13	0	18	40	32	22	35	129	9	23	26	7	65
81	5	0	9	0	14	40	27	22	35	124	3	3	9	2	17
82	5	0	9	0	14	40	21	17	35	113	1	2	7	2	12
83	5	0	7	0	12	35	21	12	35	105	0	0	2	1	3
84	5	0	2	0	7	27	15	11	25	78	0	0	1	0	1
85	5	0	2	0	7	25	15	7	11	58	0	0	0	0	0
86	5	0	1	0	6	20	15	5	10	50	0	0	0	0	0
87	1	0	1	0	2	6	10	1	10	27	0	0	0	0	0
88	0	0	0	0	0	0	5	0	1	6	0	0	0	0	0
89	0	0	0	0	0	0	5	0	0	5	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	2	6	6	15	85	135	105	80	405
100	45	56	30	18	93	1		0	0	13	0.5	133	103	00	1 105

Appendix 11: The environmental variables at the Habitat Structure Sites

17	S43	S43	S43	S43	S43	S44	S44	S44	S44	S44	S45	S45	S45	S45	S45
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
101	135	180	165	131	431	5	15	30	25	75	255	300	275	265	1095
102	130	180	190	136	456	5	15	30	30	80	290	235	295	305	1125
103	115	150	190	135	440	5	20	40	25	90	170	68	126	315	739
104	30	140	140	125	295	5	10	30	25	70	21	6	57	230	314
105	17	101	120	121	258	5	10	20	25	70	4	5	6	151	166
106	5	1	76	120	201	5	15	15	25	60	0	1	1	132	134
107	1	21	27	111	139	5	15	5	25	50	0	0	0	51	51
108	0	1	6	101	107	5	6	0	21	32	0	0	0	25	25
109	0	0	5	95	100	1	16	0	5	22	0	0	0	6	6
110	0	0	1	5	6	0	15	0	0	15	0	0	0	1	1
111	0	0	1	1	2	0	10	0	0	10	0	0	0	0	0
112	0	0	0	0	0	0	10	0	0	10	0	0	0	0	0
113	0	0	0	0	0	0	6	0	0	6	0	0	0	0	0
114	0	0	0	0	0	0	5	0	0	5	0	0	0	0	0
115	0	0	0	0	0	0	5	0	0	5	0	0	0	0	0
116	0	0	0	0	0	0	5	0	0	5	0	0	0	0	0
117	0	0	0	0	0	0	0	0_	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0_	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	- 0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0_	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	_	0	0	+
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0_	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0		0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	1 0	0	0	0	1 0	1 0

Appendix 11: The environmental variables at the Habitat Structure Sites

v y 246 S46 S46 S46 S47 S47 S47 S48		C46	CAC	CAC	CAC	C46	C 47	C 47	0.45	0.47	0.45	C40	C 40	0.40	0.40	C 40
1	V			100000					777.7	7111		140				
The color The	1	_	_				_	_		_			_	_	_	
3	_															
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21 0 0 0 0 6 0 6 0 12 47 2 0 2 51 22 0 0 0 0 0 1 0 5 0 6 36 1 0 0 37 23 0 0 0 0 1 0 1 0 2 36 1 0 0 37 24 0 0 0 0 1 0 0 0 1 1 0 0 2 25 0 <												_	_			
22 0 0 0 0 1 0 5 0 6 36 1 0 0 37 23 0 0 0 0 0 1 0 1 0 2 36 1 0 0 37 24 0 0 0 0 1 0 0 0 1 1 0<										_						
23 0 0 0 0 1 0 1 0 2 36 1 0 0 37 24 0 0 0 0 1 0 0 0 1 21 1 0 0 22 25 0<														-		
24 0 0 0 0 1 0 0 1 21 1 0 0 22 25 0 0 0 0 1 0 0 0 1 16 0 0 0 16 26 0 0 0 0 0 0 0 0 11 0 0 0 0 11 27 0 <td< td=""><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>-</td><td></td><td>_</td><td></td></td<>													-		_	
25 0 0 0 0 1 0 0 1 16 0 0 0 16 26 0 <td>-</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>_</td> <td></td> <td>-</td> <td>_</td> <td></td> <td></td>	-										_		-	_		
26 0 0 0 0 0 0 0 11 0 0 0 11 27 0 <td></td> <td></td> <td></td> <td></td> <td></td> <td>-</td> <td>_</td> <td></td> <td></td> <td></td> <td>-</td> <td></td> <td>-</td> <td></td> <td></td> <td></td>						-	_				-		-			
27 0	$\overline{}$								-		_	_	_	_		
28 0									_		_	_		_	_	
29 0 0 0 0 0 0 0 0 0 1 0 0 0 1 30 0						_		-			_				-	
30 0						-		-	-				-			
31 0						-		-			-		_		_	
32 0						-		_		_	0	_		0		
33 0											_	-	0	0		
34 0	$\overline{}$							_			_	_		0		
35 0 17 222 37 4 4 5 7 20 28 6 27 13 74 150 80 70 17 317 38 2 2 4 3 11 10 1 17 5 32 200 85 65 12 362 39 0 1 <t< td=""><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></t<>																
36 17 21 25 26 89 86 23 60 17 186 100 55 50 17 222 37 4 4 5 7 20 28 6 27 13 74 150 80 70 17 317 38 2 2 4 3 11 10 1 17 5 32 200 85 65 12 362 39 0 1 2 2 5 5 0 9 5 19 195 81 46 8 330 40 0 0 1 1 2 5 0 8 3 16 185 41 36 4 266 41 0 0 0 0 5 0 3 2 10 116 22 5 3 146 42 0 <t< td=""><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>0</td><td>0</td><td></td><td>0</td></t<>													0	0		0
37 4 4 5 7 20 28 6 27 13 74 150 80 70 17 317 38 2 2 4 3 11 10 1 17 5 32 200 85 65 12 362 39 0 1 2 2 5 5 0 9 5 19 195 81 46 8 330 40 0 0 1 1 2 5 0 8 3 16 185 41 36 4 266 41 0 0 0 0 5 0 3 2 10 116 22 5 3 146 42 0 0 0 0 1 0 3 1 5 91 18 0 3 112 43 0 0 0	\rightarrow															222
38 2 2 4 3 11 10 1 17 5 32 200 85 65 12 362 39 0 1 2 2 5 5 0 9 5 19 195 81 46 8 330 40 0 0 1 1 2 5 0 9 5 19 195 81 46 8 330 40 0 0 1 1 2 5 0 8 3 16 185 41 36 4 266 41 0 0 0 0 5 0 3 2 10 116 22 5 3 146 42 0 0 0 0 1 0 3 1 5 91 18 0 3 112 43 0 0 0 <t< td=""><td>$\overline{}$</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>70</td><td>17</td><td>317</td></t<>	$\overline{}$													70	17	317
39 0 1 2 2 5 5 0 9 5 19 195 81 46 8 330 40 0 0 0 1 1 2 5 0 8 3 16 185 41 36 4 266 41 0 0 0 0 0 5 0 3 2 10 116 22 5 3 146 42 0 0 0 0 1 0 3 1 5 91 18 0 3 112 43 0 0 0 0 1 0 3 0 4 83 14 0 2 99 44 0 0 0 0 1 0 2 0 3 67 5 0 0 72 45 0 0 0 0								1		5	32	200	85	65	12	362
40 0 0 1 1 2 5 0 8 3 16 185 41 36 4 266 41 0 0 0 0 0 5 0 3 2 10 116 22 5 3 146 42 0 0 0 0 1 0 3 1 5 91 18 0 3 112 43 0 0 0 0 1 0 3 0 4 83 14 0 2 99 44 0 0 0 0 1 0 2 0 3 67 5 0 0 72 45 0 0 0 0 1 0 0 1 57 2 0 0 59 46 0 0 0 0 0 0 0 <			$\overline{}$											46	8	
41 0 0 0 0 5 0 3 2 10 116 22 5 3 146 42 0 0 0 0 1 0 3 1 5 91 18 0 3 112 43 0 0 0 0 1 0 3 0 4 83 14 0 2 99 44 0 0 0 0 1 0 2 0 3 67 5 0 0 72 45 0 0 0 0 1 0 0 0 1 57 2 0 0 59 46 0 0 0 0 0 0 1 42 1 0 0 43 47 0 0 0 0 0 0 0 0 0 0 0<		0						0	8	3	16	185	41	36	4	266
42 0 0 0 0 1 0 3 1 5 91 18 0 3 112 43 0 0 0 0 0 1 0 3 0 4 83 14 0 2 99 44 0 0 0 0 1 0 2 0 3 67 5 0 0 72 45 0 0 0 0 1 0 0 0 1 57 2 0 0 59 46 0 0 0 0 1 0 0 0 1 42 1 0 0 43 47 0	\longrightarrow							0		2	10	116	22	5	3	146
43 0 0 0 0 0 1 0 3 0 4 83 14 0 2 99 44 0 0 0 0 0 1 0 2 0 3 67 5 0 0 72 45 0 0 0 0 1 0 0 1 57 2 0 0 59 46 0 0 0 0 1 0 0 0 1 42 1 0 0 43 47 0	\rightarrow	-		0	0			0			5	91	18	0	3	112
44 0 0 0 0 1 0 2 0 3 67 5 0 0 72 45 0 0 0 0 1 0 0 1 57 2 0 0 59 46 0 0 0 0 1 0 0 1 42 1 0 0 43 47 0 0 0 0 1 0 0 0 1 42 0 0 0 42 48 0	\rightarrow							0		0	4	83		0	2	99
45 0 0 0 0 1 0 0 0 1 57 2 0 0 59 46 0 0 0 0 1 0 0 1 42 1 0 0 43 47 0 0 0 0 1 0 0 0 1 42 0 0 0 42 48 0 <td< td=""><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>$\overline{}$</td><td>0</td><td>3</td><td>67</td><td>5</td><td>0</td><td>0</td><td>72</td></td<>									$\overline{}$	0	3	67	5	0	0	72
46 0 0 0 0 1 0 0 1 42 1 0 0 43 47 0 0 0 0 1 0 0 1 42 0 0 0 0 42 48 0<								0		0	1	57	2	0	0	59
47 0 0 0 0 1 0 0 1 42 0 0 0 42 48 0 0 0 0 0 0 0 0 41 0 0 0 41 49 0<							_	0		0	1			0	0	43
48 0 0 0 0 0 0 0 0 41 0 0 0 41 49 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 15 0 0 0 15		-				_	1	-	0	0	1	42	0	0	0	42
49 0 0 0 0 0 0 0 0 0 0 15 0 0 0 15		-								0	0	41	0	0	0	41
		_					_	0	0		0		0	0	0	15
	50	0	0	0	0	0	0			0			0	0	0	_

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S46	S46	S46	S46	S46	S47	S47	S47	S47	S47	S48	S48	S48	S48	S48
	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
51	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
52	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	45	26	12	17	100	30	75	21	0	167	18	0	0	0	0
58	43	6	2	2	14	26	1	5	41	36	18	23	0	5	37 43
59	1	2	0	0	3	10	0	1	0	11	13	9	0	0	22
60	0	1	0	0	1	1	0	0	0	1	12	5	0	0	17
61	0	1	0	0	1	0	0	0	0	0	12	3	0	0	15
62	0	0	0	0	0	0	0	0	0	0	7	2	0	0	9
63	0	0	0	0	0	0	0	0	0	0	7	1	0	0	8
64	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
65	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
66	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
67	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
68	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
69	0	0	0	0	0	0	0	0	0	0	6	0	0	0	6
70	0	0	0	0	0	0	0	0	0	0	6	0	0	0	6
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	13	25	30	7	75	50	31	60	30	171	4	21	10	1	36
79	28	6	45	2	81	110	95	140	55	400	12	31	20	5	68
80	27	6	27	2	62	130	130	140	60	460	21	31	5	10	67
81	6	2	16	0	24	115	115	140	60	430	21	31	0	10	62
82	2	0	15	0	17	101	75	101	75 70	352 296	20	21	0	5	46
83	0	0	5	0	5	51	46	81	50	228	16	25	0	0	42
84	0	0	0	0	0	40	31	80	45	196	21	16	0	0	37
85	0	0	0	0	0	40	1	80	16	137	17	16	0	0	33
86	0	0	0	0	0	5	0	10	6	21	11	16	0	0	27
88	0	0	0	0	0	1	0	5	2	8	11	11	0	0	22
89	0	0	0	0	0	0	0	5	1	6	7	11	0	0	18
90	0	0	0	0	0	0	0	0	0	0	2	1	0	0	3
91	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
92	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	55	80	85	41	261	0	0	0	30	30	21	15	65	16	117

Appendix 11: The environmental variables at the Habitat Structure Sites

v	S46	S46	S46	S46	S46	S47	S47	S47	S47	S47	S48	S48	S48	S48	S48
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
101	175	220	240	65	700	0	0	0	80	80	61	35	230	95	421
102	210	220	115	65	610	0	0	0	80	80	66	50	230	90	436
103	235	210	75	70	590	0	0	0	75	75	72	50	150	75	347
104	220	166	41	65	492	0	0	0	55	55	95	75	137	65	372
105	210	170	26	35	441	0	0	0	41	41	110	80	62	56	308
106	176	156	21	25	378	0	0	0	30	30	120	90	40	51	301
107	146	155	20	21	342	0	0	0	20	20	130	90	1	2	223
108	97	155	5	16	273	0	0	0	10	10	160	80	0	0	240
109	81	155	1	2	239	0	0	0	2	2	105	30	0	0	135
110	66	90	0	2	158	0	0	0	0	0	130	20	0	0	150
111	55	86	0	0	141	0	0	0	0	0	125	20	0	0	145
112	51	85	0	0	136	0	0	0	0	0	45	15	0	0	60
113	40	85	0	0	125	0	0	0	0	0	30	11	0	0	41
114	40	85	0	0	125	0	0	0	0	0	10	10	0	0	20
115	1	5	0	0	6	0	0	0	0	0	10	5	0	0	15
116	0	1	0	0	1	0	0	0	0	0	5	5	0	0	10
117	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0_	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0_	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S49	S49	S49	S49	S49	S50	S50	S50	S50	S50	S51	S51	S51	S51	CEI
V	pa	pb	pc	pd	all	pa	pb	pc	pd	all	pa	pb	pc	pd	S51 all
1	90	35	125	50	300	90	85	45	80	300	66	60	60	80	266
2	130	105	35	35	305	85	75	25	125	310	32	18	26	27	103
3	0	0	0	0	0	0	0	0	0	0	0	5	11	1	17
4	41	50	95	50	236	65	65	40	50	220	0	6	12	6	24
5	26	46	30	126	228	2	50	165	55	272	21	71	90	45	227
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	2	6	8	0	1	0	0	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	5	35	10	0	50	30	6	0	1	37	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	10	18	18	20	66
15	31	41	40	60	172	50	55	85	55	1015	85	30	27	75	217
16	21	26	7	26	80	65	22	14	25	126	5	18	9	32	64
17	2	4	2	8	16	42	9	7	4	62	5	14	5	3	27
18	0	3	0	3	6	8	2	1	1	12	5	14	4	3	26
19	0	2	0	1	3	2	0	0	0	2	5	9	4	3	21
20	0	1	0	1	2	0	0	0	0	0	5	7	4	3	19
21	0	1	0	1	2	0	0	0	0	0	5	2	3	1	11
22	0	1	0	0	1	0	0	0	0	0	1	2	0	1	4
23	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
24	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
25	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	15	60	65	80	220	65	45	50	31	191	155	55	41	60	311
37	15	31	46	40	132	75	46	26	13	160	13	17	21	1	52
38	0	8	9	19	36	35	18	5	5	63	0	10	0	0	10
39	0	7	2	9	18	9	9	5	4	27	0	5	0	0	5
40	0	3	2	5	10	5	5	2	2	14	0	5	0	0	5
41	0	3	2	3	8	3	5	0	1	9	0	0	0	0	0
42	0	2	2	3	7	3	2	0	1	6	0	0	0	0	0
43	0	2	2	1	5	2	2	0	1	5	0	0	0	0	0
44	0	1	1	1	3	2	1	0	1	4	0	0	0	0	0
45	0	1	1	0	2	2	0	0	0	2	0	0	0	0	0
46	0	1	0	0	1	2	0	0	0	2	0	0	0	0	0
47	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S49	S49	S49	S49	S49	S50	S50	S50	S50	S50	S51	S51	S51	S51	S51
	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	21	22	26	22	91	55	70	40	85	250	0	0	0	65	65
58	4	9	8	9	30	75	45	17	40	177	0	0	0	55	55
59	3	1	3	4	_ 11	70	13	8	5	96	0	0	0	25	25
60	3	1	3	3	-11	40	5	4	5	54	0	0	0	30	30
61	3	1	2	3	9	9	5	4	5	23	0	0	0	10	10
62	0	1	2	2	5	4	4	4	5	17	0	0	0	5	5
63	0	0	2	2	4	4	4	3	5	16	0	0	0	5	5
64	0	0	0	2	2	3	3	2	4	12	0	0	0	0	0
65	0	0	0	2	3	3	3	1	1	8	0	0	0	0	0
66	0	0	0	2	2	3	3	0	1	7	0	0	0	0	0
67	0	0	0	1	1	3	2	0	0	5	0	0	0	0	0
68	0	0	0	1	1	1	2	0	0	3	0	0	0	0	0
69	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0
70	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0
71	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
72	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
73	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	75	80	51	65	271	16	20	5	0	41	50	140	36	35	261
79	155	165	100	115	535	16	40	5	0	61	51	145	56	20	272
80	180	210	100	120	610	4	51	5	0	60	36	91	55	0	182
81	190	185	80	65	520	4	56	1	0	61	22	26	45	0	93
82	75	135	66	47	323	2	22	1	0	25	5	20	20	0	80
83	31	55	25	30	141	2	20	1	0	23	0	0	5	-	37
84	2	6	5	6	19	2	15	0	0	18	0	0	5	0	5
85	0	2	5	1	8		5	0	0	7	0	0	5	0	5
86	0	0	0	0	0	0	1	0	0	6	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90			0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
\rightarrow	75	25	25	5	130	41	31	21	12	105	70	135	195	90	400
100	13	23	23	3	130	71	31	21	12				1	/0	100

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S49	S49	S49	S49	S49	S50	S50	S50	S50	S50	S51	S51	S51	S51	S51
	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
101	140	115	60	10	225	125	71	37	37	260	120	170	280	120	570
102	120	125	55	10	310	130	80	22	27	259	120	170	250	140	540
103	90	125	10	5	230	135	110	12	27	284	120	120	161	140	401
104	40	130	5	5	180	106	76	12	36	230	20	61	155	145	236
105	6	100	1	1	108	91	62	8	31	192	0	0	150	90	150
106	1	100	0	1	102	46	41	1	21	116	0	0	85	5	85
107	0	91	0	0	91	31	26	0	6	63	0	0	80	0	80
108	0	90	0	0	90	22	7	0	5	34	0	0	10	0	10
109	0	65	0	0	65	22	3	0	1	26	0	0	5	0	5
110	0	45	0	0	45	7	1	0	1	9	0	0	0	0	0
111	0	45	0	0	45	2	0	0	0	2	0	0	0	0	0
112	0	11	0	0	11	0	0	0	0	0	0	0	0	0	0
113	0	11	0	0	11	0	0	0	0	0	0	0	0	0	0
114	0	6	0	0	6	0	0	0	0	0	0	0	0	0	0
115	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	35	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	35	0	0	0	0	0	- 0	0	0	0	0
124	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0
125	0	0_	0	0	40	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0
127	0	0_	0	0	40	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	55	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0_	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S52	S52	S52	S52	S52	S53	S53	S53	S53	S53	S54	S54	CEA	CEA	S54
V	pa	pb	pc	pd	all	pa	pb	pc	pd	all	pa	pb	S54 pc	S54 pd	all
1	41	9	13	37	100	170	130	270	215	785	191	305	160	135	791
2	45	45	30	36	156	115	95	75	110	395	56	90	56	91	293
3	16	2	12	8	38	0	0	2	0	2	2	0	12	1	15
4	35	36	75	46	192	0	0	1	0	1	2	2	16	1	21
5	120	195	150	240	705	0	0	3	2	5	145	10	195	322	672
6	1	0	0	1	2	0	0	0	1	1	0	0	0	0	0
7	0	0	0	0	0	0	0	1	8	9	0	0	0	0	0
8	0	6	0	0	6	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
14	2	21	15	17	55	0	0	0	0	0	2	0	0	0	2
15	91	110	170	56	427	6	12	20	1	39	0	0	0	0	0
16	91	110	170	66	437	0	0	0	1	1	0	0	0	0	0
17	72	107	175	66	420	0	0	0	0	0	0	0	0	0	0
18	52	102	120	53	327	0	0	0	0	0	0	0	0	0	0
19	42	101	105	33	281	0	0	0	0	0	0	0	0	0	0
20	1	91	6	33	131	0	0	0	0	0	0	0	0	0	0
21	1	30	0	38	69	0	0	0	0	0	0	0	0	0	0
22	1	0	0	8	9	0	0	0	0	0	0	0	0	0	0
23	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0
24	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
25	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
\rightarrow	30	55	30	66	181	50	65	71	41	227	8	41	12	3	64
36	21	55	35	71	182	17	9	5	9	40	8	32	12	11	63
38	11	27	30	86	154	4	1	1	1	7	1	26	3	6	36
39	11	27	20	73	131	1	1	1	0	3	0	2	1	1	4
40	10	18	16	63	107	1	1	0	0	2	0	0	0	0	0
41	1	13	6	53	73	0	0	0	0	0	0	0	0	0	0
42	1	13	2	18	34	0	0	0	0	0	0	0	0	0	0
43	1	7	1	5	14	0	0	0	0	0	0	0	0	0	0
44	1	2	1	4	8	0	0	0	0	0	0	0	0	0	0
45	1	1	1	4	7	0	0	0	0	0	0	0	0	0	0
46	0	1	1	2	4	0	0	0	0	0	0	0	0	0	0
47	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0
48	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
49	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
50	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

Pa Pb Pb Pd all Pa Pb Pc Pd all Pa Pb Pb Pb Pb Pb Pb Pb		S52	S52	S52	S52	S52	S53	S53	S53	S53	S53	S54	S54	S54	S54	S54
ST	V													The state of		
S3	51	0	-	1	_			_					_			
S4	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S55	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S6		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S7			0	0	0	0	0	0	0	0	0	0	0	0	0	0
S8									0	_		0				
S9																
GO																
61 5 0 5 7 17 0				-												
G2					_				$\overline{}$				$\overline{}$			
63 0 0 0 1 1 0																
64 0																
65 0 0 0 0 0 0 0 0 0 0 0 0 0	$\overline{}$			_							_					
66 0			_				_									
67 0					_											
68 0															_	
69 0	$\overline{}$								_					-		
70 0		_														
71 0				_			_	_						_		
72 0										_					_	
73 0				_			0	-		0			0	0		
74 0				0	0	0	0	0	0	0	0	0	0	0	0	0
76 0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77 0	75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78 47 18 12 2 79 2 1 0 0 3 6 8 26 6 46 79 52 22 12 2 88 2 5 0 0 7 20 21 31 6 83 80 23 22 7 2 54 1 5 0 0 6 30 31 30 11 102 81 24 17 7 2 50 0 5 0 0 5 20 22 1 10 53 82 29 8 1 2 40 0 0 0 0 0 0 0 10 18 83 13 9 1 2 25 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 <td></td> <td>0</td> <td></td> <td>0</td> <td>0</td> <td>0</td> <td>0</td> <td>0</td> <td></td> <td>0</td> <td></td> <td></td> <td></td> <td></td> <td>-</td> <td></td>		0		0	0	0	0	0		0					-	
79 52 22 12 2 88 2 5 0 0 7 20 21 31 6 83 80 23 22 7 2 54 1 5 0 0 6 30 31 30 11 102 81 24 17 7 2 50 0 5 0 0 5 20 22 1 10 53 82 29 8 1 2 40 0 0 0 0 5 3 0 10 18 83 13 9 1 2 25 0 0 0 0 0 0 0 0 10 18 83 13 2 1 1 17 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0								-	-	_	+	-	-		-	_
80 23 22 7 2 54 1 5 0 0 6 30 31 30 11 102 81 24 17 7 2 50 0 5 0 0 5 20 22 1 10 53 82 29 8 1 2 40 0 0 0 0 5 3 0 10 18 83 13 9 1 2 25 0<					_			+	+	-					_	-
81 24 17 7 2 50 0 5 0 0 5 20 22 1 10 53 82 29 8 1 2 40 0 0 0 0 5 3 0 10 18 83 13 9 1 2 25 0					-		_	_	-	-	-				-	
82 29 8 1 2 40 0 0 0 0 5 3 0 10 18 83 13 9 1 2 25 0					-		-									
83 13 9 1 2 25 0 0 0 0 0 0 0 10 10 84 13 2 1 1 17 0					-		_		_	-				_	-	
84 13 2 1 1 17 0							_	+						-		
85 8 2 0 1 11 0				_			_	-	_	-				-	-	
86 7 6 0 1 14 0				_	-			_	_	-		-	-	_		
87 0 0 0 1 1 0																
88 0					_											
89 0						_				_			+	+		
90 0										_						
91 0										-						
92 0										0		0	0	0	0	
93 0										0	0	0	0	0	0	0
94 0									0	0	0	0		0	0	0
95 0	\rightarrow					0	0	0	0	0					-	0
96 0	\rightarrow	\rightarrow			0	0	0			_				_		0
97 0	\rightarrow				0	0	0					+	-			
98 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0			0	0	0	0				_						
		0	0							_						
	100	75	36	25	16	152	130	175	55	110	470	75	10	20	22	127

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S52	S52	S52	S52	S52	S53	S53	S53	S53	S53	S54	S54	S54	S54	S54
	pa	pb	рс	pd	all	pa	pb	pc	pd	all	pa	pb	рс	pd	all
101	130	65	20	70	285	120	165	65	125	475	130	25	46	50	251
102	160	90	20	80	350	140	151	40	80	411	65	26	12	150	253
103	190	80	30	90	390	90	155	30	61	336	50	5	15	170	240
104	210	60	40	85	395	6	70	20	51	147	10	0	10	215	235
105	215	0	40	70	325	0	65	5	5	75	0	0	- 1	216	217
106	90	0	40	70	200	0	65	0	0	65	0	0	0	95	95
107	10	0	40	35	85	0	65	0	0	65	0	0	0	85	85
108	1	0	40	15	56	0	0	0	0	0	0	0	0	85	85
109	0	0	60	0	60	0	0	0	0	0	0	0	0	10	10
110	0	0	60	0	60	0	0	0	0	0	0	0	0	5	5
111	0	0	60	0	60	0	0	0	0	0	0	0	0	0	0
112	0	0	60	0	60	0	0	0	0	0	0	0	0	0	0
113	0	0	60	0	60	0	0	0	0	0	0	0	0	0	0
114	0	0	60	0	60	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	5	5	0	0	0	0	0
124	0	0	0	0	0	0	0	0	10	10	0	0	0	0	0
125	0	0	0	0	0	0	0	0	10	10	0	0	0	0	0
126	0	0	0	0	0	0	0	0	10	10	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	10	10	0	0	0	0	0
134	0	0	0	0	0	0	0	0	10	10	0	0	0	0	0
135	0	0	0	0	0	0	0	0	10	10	0	0	0	0	0
136	0	0	0	0	0	0	0	0	10	10	0	0	0	0	0
137	0	0	0	0	0	0	0	0	80	80	0	0	0	0	0
138	0	0	0	0	0	0	0	0	80	80	0	0	0	0	0
139	0	0	0	0	0	0	0	0	80	80	0	0	0	0	0
140	0	0	0	0	0	0	0	0	80	80	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

X.7	S55	S55	S55	S55	S55	S56	S56	S56	S56	S56	S57	S57	S57	S57	S57
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
1	140	145	200	115	600	275	255	215	255	1000	95	105	90	45	335
2	30	55	65	40	190	65	85	145	140	435	105	47	125	80	357
3	9	5	0	1	15	31	26	5	5	67	31	45	35	35	146
4	4	1	0	1	6	17	22	3	4	49	60	130	55	90	335
5	0	5	0	36	41	0	36	0	1	37	21	50	30	70	171
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	1	0	2	1	4	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	5	1	0	0	6	12	7	0	0	19	70	25	50	70	215
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	1	4	5	1	0	0	0	1	0	0	0	0	0
16	0	0	1	4	5	1	0	0	0	1	0	0	0	0	0
17	0	0	1	2	3	0	0	0	0	0	0	0	0	0	0
18	0	0	1	2	3	0	0	0	0	0	0	0	0	0	0
19	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	36	149	0	10	5	0	15
36	120	155	190	300	765	26	22	65	_		0	2	1	0	3
37	65	100	106	53	324	18	63	23	28	132	0	2	1	0	3
38	18	27	9	4	81	9	5	4	14	26	0	2	0	0	2
39	5	5	5	4	19	4	4	4	5	16	0	2	0	0	2
40	2	4	5	3	14	3	4	4	5	16	0	2	0	0	2
41	2	4_	4	2	12	3	4	3	3	13	0	2	0	0	2
42	0	2	3	1	6	3	2	2	2	9	0	2	0	0	2
43	0	0	3	1	4	2	1	2	2	7	0	2	0	0	2
44	0	0	2	0	2	1	0	0	1	2	0	1	0	0	1
45	0	0	1	0	1		0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0								0

Appendix 11: The environmental variables at the Habitat Structure Sites

	S55	S55	S55	S55	S55	S56	S56	S56	S56	S56	S57	S57	S57	S57	S57
V	pa	pb	рс	pd	all	pa	pb	рс	pd	all	pa	pb	рс	pd	all
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	160	115	18	18	311	2	3	5	5	15	30	12	0	2	44
58	101	60	23	17	201	2	1	9	3	15	40	4	0	2	46
59	9	34	17	7	67	1	1	9	2	13	22	3	0	2	27
60	5	5	42	7	59	0	1	5	1	7	8	1	0	2	11
61	2	5	3	3	13	0	1	3	1	5	7	1	0	2	2
62	2	5	3	3	13	0	1	2	0	3	1	1	0	0	3
63	1	3	2	2	8	0	1	1	0	2	0	0	0	0	0
64	1	2	1	0	4	0	0	0	0	0	0	0	0	0	0
65	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0
66	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0
67	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72 73	_	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	41	0	0	0	0	40	35	55	70	200	25	30	55	45	155
79	30	0	0	0	0	70	75	120	165	430	45	26	105	75	251
80	8	0	0	0	0	126	145	136	220	627	22	13	105	65	205
81	1	0	0	0	0	85	115	100	220	520	5	4	36	35	80
82	0	0	0	0	0	20	66	91	170	347	2	1	22	13	38
83	0	0	0	0	0	6	6	41	65	93	1	1	8	10	20
84	0	0	0	0	0	1	1	6	40	48	1	1	2	1	5
85	0	0	0	0	0	0	0	2	21	23	1	0	1	0	2
86	0	0	0	0	0	0	0	0	5	5	1	0	0	0	1
87	0	0	0	0	0	0	0	0	0	0	1	0	0	0	- 1
88	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	25	41	15	0	0	77	65	60	65	75	265
100	0	5	25	0	23	41	13	0		, ,	05		0,5	, 5	203

Appendix 11: The environmental variables at the Habitat Structure Sites

V	S55	S55	S55	S55	S55	S56	S56	S56	S56	S56	S57	S57	S57	S57	S57
	pa	pb	pc	pd	all	pa	pb	рс	pd	all	pa	pb	pc	pd	all
101	0	1	45	0	45	135	55	0	0	310	130	136	175	171	612
102	0	0	60	0	60	110	46	0	5	217	85	91	100	186	462
103	0	0	80	0	80	95	60	0	5	202	81	36	70	61	248
104	0	0	80	0	80	66	30	0	0	121	81	52	41	22	196
105	0	0	5	0	5	60	20	0	0	87	66	12	21	17	116
106	0	0	5	0	5	51	10	0	0	62	50	5	16	8	79
107	0	0	1	0	1	60	1	0	0	61	36	1	10	7	54
108	0	0	1	0_	1	65	0	0	0	65	13	0	0	5	18
109	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
116	0	0	0	0_	0	0	0	0	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	5	0	0	0	5
125	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
126	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
127	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	0	0	0	0	0	0	0	0	0	0_	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 11: The environmental variables at the Habitat Structure Sites

6	S58	S58	S58	S58	S58	S59	S59	S59	S59	S59	S60	S60	S60	S60	S60
V	pa	pb	pc	pd	all	pa	pb	pc	pd	all	pa	pb	pc	pd	all
1	55	35	71	65	226	90	200	95	145	530	160	125	115	110	510
2	50	155	61	85	351	185	120	95	70	470	50	60	40	130	280
3	45	30	85	25	185	0	6	0	0	6	20	21	26	30	97
4	70	60	135	55	320	1	10	0	0	11	21	21	13	21	76
5	50	17	35	170	272	20	0	0	6	26	30	95	95	36	256
6	0	5	1	0	6	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	70	31	5	15	121	0	0	0	0	0	35	45	50	0	130
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	2	15	16	0	33	0	0	0	0	0
16	0	0	0	0	0	2	20	12	0	34	0	0	0	0	0
17	0	0	0	0	0	1	5	7	0	13	0	0	0	0	0
18	0	0	0	0	0	0	1	5	0	6	0	0	0	0	0
19	0	0	0	0	0	0	0	5	0	5	0	0	0	0	0
20	0	0	0	0_	0	0	0	1	0	1	0	0	0	0	0
21	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	136	135	85	230	205	655	36	46	65	30	177
36	25	60	40	11	152	45	21	170	75	311	13	13	8	9	43
37	25	70	15	8	84	17	12	31	17	77	4	4	1	4	13
38	1	50	11	3	33	9	3	8	4	24	3	2	0	2	2
39	3	16	11	5	20	5	1	8	4	18	2	2	0	2	6
40		3	11	3	20	0	1	3	3	7	1	1	0	2	4
41	3	1	6	3	13	0	1	2	2	5	1	1	0	2	4
42	2	0	2	3	7	0	1	2	1	4	0	0	0	2	2
43	2	0	1	2	5	0	1	0	0	1	0	0	0	2	2
44	2	0	1	1	4	0	0	0	0	0	0	0	0	2	2
45	2	0	1	1	4	0	0	0	0	0	0	0	0	2	2
46	1	0	0	0	1	0	0	0	0	0	0	0	0	2	2
$\overline{}$	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
48	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
		0	0	0	0	0	0	0	0	0	0	0	0	2	2
50	0	0	U	U	0						7				

Appendix 11: The environmental variables at the Habitat Structure Sites

V 51 52 53 54 55 56 57	\$58 pa 0 0 0 0	S58 pb 0 0	S58 pc 0	S58 pd 0	all	pa	pb	рс	pd	all	pa	pb	рс	S60 pd	S60
52 53 54 55 56	0 0	0		0	_ ^		-	P	pu	un	pa	ρυ	pc	pu	all
53 54 55 56	0		0		0	0	0	0	0	0	0	0	0	2	2
54 55 56	0	0		0	0	0	0	0	0	0	0	0	0	1	1
55 56			0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
~ 1	10	0	7	3	20	25	5	5	15	50	30	40	45	27	142
58	6	0	2	3	11	15	5	1	7	28	13	21	14	9	57
59	1	0	2	3	6	2	1	0	6	9	7	4	1	2	14
60	0	0	1	3	4	2	0	0	2	4	9	2	0	2	13
61	0	0	1	3	4	1	0	0	1	2	1	0	0	0	1
62	0	0	0	2	2	1	0	0	0	1	0	0	0	0	0
63	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0
64	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0
65	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0_	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	50	151	21	35	25	35	0
78	55	65	41	35	196	25	30	46 65	65	200	21	35	21	36	116
79	115	115	56	70	356	30	37	66	66	200	13	26	13	41	93
80	140	15	30	57	332	22	42	32	71	167	4	17	3	31	55
81	72	36	11	11	130 56	22	40	31	51	144	1	7	1	27	36
82	20	36	1	1	11	17	45	20	30	112	1	0	1	27	29
83	6	5	0	0	2	12	50	15	26	103	1	0	1	11	13
84	1	1	0	0	1	12	31	15	5	63	1	0	1	6	8
85	0			0	1	12	21	5	1	39	0	0	1	5	6
86	0	1	0	0	1	2	20	0	0	22	0	0	1	5	6
87	0	0	0	0	0	2	20	0	0	21	0	0	1	5	6
88	0	0	0	0	0	1	20	0	0	20	0	0	0	5	5
90	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	70	45	35	40	190	20	30	20	10	80	90	26	30	85	231

Appendix 11: The environmental variables at the Habitat Structure Sites

	S58	S58	S58	S58	S58	S59	S59	S59	S59	S59	S60	S60	S60	S60	S60
V	pa	pb	рс	pd	all	pa	pb	pc	pd	all	pa	pb	рс	pd	all
101	185	115	105	61	466	50	61	46	10	167	215	66	60	235	576
102	175	135	75	115	500	65	70	46	26	207	235	61	55	225	576
103	105	101	61	141	408	50	80	45	31	206	230	46	60	180	516
104	75	51	56	55	237	35	70	50	36	191	235	46	55	196	532
105	57	26	31	75	189	35	80	45	20	180	115	40	30	131	316
106	38	6	5	30	79	35	65	50	20	170	10	30	20	120	180
107	2	5	1	46	58	30	71	35	20	156	1	20	20	120	161
108	0	1	0	5	7	30	91	11	10	142	0	20	20	110	150
109	0	0	0	1	1	20	50	10	10	90	0	5	1	0	6
110	0	0	0	0	0	15	30	10	10	65	0	0	0	0	0
111	0	0	0	0	0	10	35	10	10	65	0	0	0	0	0
112	0	0	0	0	0	10	20	10	5	45	0	0	0	0	0
113	0	0	0	0	0	10	6	10	5	31	0	0	0	0	0
114	0	0	0	0	0	6	2	6	1	15	0	0	0	0	0
115	0	0	0	0	0	1	2	1	1	10	0	0	0	0	0
116	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
117	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135 136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	U	0_	U	0	0	0							10-15		

Appendix 12. Partial correlations (pcc) on \log_{x+1} transformed data used for testing the hypotheses that some types of heterogeneity affect the number of species, and species abundances, independently of total complexity (Section 6.9.2). Correlations are measured between pairs of variables whilst holding total complexity (i.e. the sum complexity of all variables) constant. Results are for (1) combined data from sand, steppe and garigue habitats, from wet and dry periods combined, and wet and dry periods separately, and (2) for each habitat using combined data from wet and dry periods, and wet and dry periods separately. Only significant correlations are shown; these are 2-tailed for all cases, and significance levels are indicated as: * (0.05), ** (0.01), *** (0.001 or <0.001). See Table 6.5 for full list of environmental variables and Table 6.1 for list of sites with habitat types and periods.

Environmental Variable	pcc	sig	Environmental Variable	рсс	sig
leaf litter	0.062	*	annual 60 to 70cm layer	0.070	**
rubble	0.154	***	annual 70 to 80cm layer	0.057	*
other wood	0.061	ak	herbaceous 140 to 150cm layer	-0.057	*
refuse	0.077	**	shrub 0 to 10cm layer	-0.072	**
green grass 10 to 20cm layer	0.100	***	shrub 10 to 20cm layer	-0.072	**
green grass 20 to 30cm layer	0.094	***	shrub 20 to 30cm layer	-0.071	* *
green grass 30 to 40cm layer	0.098	***	shrub 30 to 40cm layer	-0.078	* *
green grass 40 to 50cm layer	0.097	***	shrub 40 to 50cm layer	-0.093	**
green grass 50 to 60cm layer	0.091	**	shrub 50 to 60cm layer	-0.111	**
green grass 60 to 70cm layer	0.080	* *	shrub 60 to 70cm layer	-0.128	**
dry grass 20 to 30cm layer	0.063	*	shrub 70 to 80cm layer	-0.111	**
dry grass 30 to 40cm layer	0.076	**	shrub 80 to 90cm layer	-0.106	**:
dry grass 40 to 50cm layer	0.084	**	shrub 90 to 100cm layer	-0.111	**:
dry grass 50 to 60cm layer	0.073	**	shrub 100 to 110cm layer	-0.103	**
dry grass 60 to 70cm layer	0.069	**	shrub 110 to 120cm layer	-0.092	**:
dry grass 70 to 80cm layer	0.077	**	shrub 120 to 130cm layer	-0.078	**
dry grass 80 to 90cm layer	0.070	**	shrub 130 to 140cm layer	-0.073	**
dry grass 90 to 100cm layer	0.069	**	shrub 140 to 150cm layer	-0.065	**
annual 50 to 60cm layer	0.059	*	shrub 150 to 160cm layer	-0.066	**

degre	ees of free	dom = 5	<u>ue</u> combined: WET sites (<i>n</i> qu 597 for each variable)		
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig
leaf litter	0.089	**	herbaceous 0 to 10cm layer	0.088	*
shingle	-0.126	**	herbaceous 10 to 20cm layer	0.091	*
rubble	0.192	***	shrub 0 to 10cm layer	-0.203	**
other wood	0.087	*	shrub 10 to 20cm layer	-0.192	**
lichen	-0.132	***	shrub 20 to 30cm layer	-0.185	**:
green grass 10 to 20cm layer	0.143	***	shrub 30 to 40cm layer	-0.172	**
green grass 20 to 30cm layer	0.102	**	shrub 40 to 50cm layer	-0.175	**
green grass 30 to 40cm layer	0.101	**	shrub 50 to 60cm layer	-0.180	**:
green grass 40 to 50cm layer	0.105	**	shrub 60 to 70cm layer	-0.171	***
green grass 50 to 60cm layer	0.098	**	shrub 70 to 80cm layer	-0.136	***
green grass 60 to 70cm layer	0.085	*	shrub 80 to 90cm layer	-0.140	***
dry grass 0 to 10cm layer	0.166	***	shrub 90 to 100cm layer	-0.140	***
dry grass 10 to 20cm layer	0.247	***	shrub 100 to 110cm layer	-0.117	**
dry grass 20 to 30cm layer	0.182	***	shrub 110 to 120cm layer	-0.091	*
dry grass 30 to 40cm layer	0.136	***	shrub 190 to 200cm layer	-0.085	*
dry grass 40 to 50cm layer	0.091	**	tree >200cm layer	-0.103	* *
annual 0 to 10cm layer	0.106	*			

Environmental Variable	pcc	sig	Environmental Variable	pcc	sig
soil	-0.094	*	annual 70 to 80cm layer	0.080	*
rock	0.125	**	herbaceous 80 to 90cm layer	-0.085	*
rubble	0.094	*	herbaceous 90 to 100cm layer	-0.099	**
refuse	0.152	***	herbaceous 100 to 110cm layer	-0.105	**
green grass 20 to 30cm layer	0.097	**	herbaceous 110 to 120cm layer	-0.088	*
green grass 30 to 40cm layer	0.096	**	herbaceous 120 to 130cm layer	-0.082	*
green grass 40 to 50cm layer	0.086	*	shrub 60 to 70cm layer	-0.080	*
green grass 50 to 60cm layer	0.085	*	shrub 70 to 80cm layer	-0.081	*
dry grass 0 to 10cm layer	-0.143	***	shrub 100 to 110cm layer	-0.090	*
dry grass 10 to 20cm layer	-0.132	***	shrub 110 to 120cm layer	-0.100	*
dry grass 70 to 80cm layer	0.105	* *	shrub 120 to 130cm layer	-0.104	*
dry grass 80 to 90cm layer	0.112	**	shrub 130 to 140cm layer	-0.103	*
annual 60 to 70cm layer	0.090	*	shrub 140 to 150cm layer	-0.090	*

<i>Jumber of Species.</i> Sand: WET and DRY sites (n quadrats= 400; degrees of freedom = 397 for each variable)									
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig				
soil	-0.124	**	green grass 10 to 20cm layer	0.277	***				
leaf litter	0.128	**	green grass 20 to 30cm layer	0.099	×				
shingle	-0.276	***	dry grass 0 to 10cm layer	0.104	*				
stone	-0.120	**	herbaceous 10 to 20cm layer	0.107	*				
rock	0.124	**	tree >200cm layer	-0.177	***				
green grass 0 to 10cm layer	0.156	**		1116					

Number of Species. Sand: WET sites (n quadrats= 200; degrees of freedom = 197 for each variable)									
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig				
soil	-0.146	*	dry grass 0 to 10cm layer	0.363	***				
leaf litter	0.148	*	dry grass 10 to 20cm layer	0.272	***				
shingle	-0.284	***	dry grass 20 to 30cm layer	0.203	**				
rock	0.190	**	annual 0 to 10cm layer	0.168	**				
green grass 0 to 10cm layer	0.140	*	tree >200cm layer	-0.264	***				
green grass 10 to 20cm layer	0.242	***		THE PAR	77.				

Number of Species. Sand: DRY sites (n quadrats= 200; degrees of freedom = 197 for each variable)								
Environmental Variable	рсс	sig	Environmental Variable	pec	sig			
shingle	-0.292	***	dry grass 10 to 20cm layer	-0.182	**			
green grass 0 to 10cm layer	0.153	**	annual 10 to 20cm layer	-0.142	*			
green grass 10 to 20cm layer	0.195	**	annual 60 to 70cm layer	0.144	*			
green grass 20 to 30cm layer	0.163	**						

Number of Species. Steppe: WET and DRY sites (n quadrats= 400; degrees of freedom = 397 for each variable)								
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig			
soil	-0.248	***	herbaceous 0 to 10cm layer	0.184	***			
leaf litter	0.126	**	herbaceous 10 to 20cm layer	0.174	**			
shingle	0.103	*	herbaceous 20 to 30cm layer	0.111	*			
stone	0.203	***	shrub 40 to 50cm layer	-0.115	*			
rock	0.309	***	shrub 50 to 60cm layer	-0.105	*			
rubble	0.201	***	shrub 110 to 120cm layer	-0.105	*			
refuse	0.100	*	shrub 120 to 130cm layer	-0.107	*			
bryophytes	0.140	**	shrub 130 to 140cm layer	-0.107	*			
green grass 0 to 10cm layer	-0.107	*	shrub 150 to 160cm layer	-0.107	*			
dry grass 0 to 10cm layer	-0.164	***	shrub 160 to 170cm layer	-0.105	*			

Number of Species. Steppe: WET (n quadrats= 200; degrees of freedom = 197 for each variable)								
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig			
soil	-0.169	*	shrub 30 to 40cm layer	-0.281	**:			
leaf litter	0.242	***	shrub 40 to 50cm layer	-0.280	**:			
rock	0.142	*	shrub 50 to 60cm layer	-0.271	**:			
rubble	0.178	**	shrub 60 to 70cm layer	-0.279	**:			
bryophytes	0.218	**	shrub 70 to 80cm layer	-0.267	**:			
lichen	-0.233	***	shrub 80 to 90cm layer	-0.250	**:			
green grass 10 to 20cm layer	0.237	***	shrub 90 to 100cm layer	-0.254	**:			
green grass 20 to 30cm layer	0.142	*	shrub 100 to 110cm layer	-0.248	**:			
dry grass 40 to 50cm layer	-0.142	*	shrub 110 to 120cm layer	-0.248	**:			
dry grass 50 to 60cm layer	-0.162	*	shrub 120 to 130cm layer	-0.233	**:			
dry grass 60 to 70cm layer	-0.221	**	shrub 130 to 140cm layer	-0.233	**:			
dry grass 70 to 80cm layer	-0.189	**	shrub 140 to 150cm layer	-0.233	**:			
dry grass 80 to 90cm layer	-0.181	**	shrub 150 to 160cm layer	-0.233	**:			
dry grass 90 to 100cm layer	-0.141	*	shrub 160 to 170cm layer	-0.233	**:			
annual 10 to 20cm layer	0.161	*	shrub 170 to 180cm layer	-0.233	**			
shrub 0 to 10cm layer	-0.272	***	shrub 180 to 190cm layer	-0.233	**:			
shrub 10 to 20cm layer	-0.250	***	shrub 190 to 200cm layer	-0.233	**:			
shrub 20 to 30cm layer	-0.272	***						

Number of Species. Steppe: DRY (n quadrats= 200; degrees of freedom = 197 for each variable)								
Environmental Variable	рсс	sig	Environmental Variable	pcc	sig			
soil	-0.339	***	dry grass 10 to 20cm layer	-0.260	***			
shingle	0.293	***	dry grass 20 to 30cm layer	-0.170	**			
stone	0.411	***	annual 0 to 10cm layer	-0.159	*			
rock	0.494	***	herbaceous 0 to 10cm layer	0.240	***			
rubble	0.228	***	herbaceous 10 to 20cm layer	0.216	**			
green grass 0 to 10cm layer	-0.258	***	herbaceous 20 to 30cm layer	0.194	**			
green grass 10 to 20cm layer	-0.178	**	herbaceous 30 to 40cm layer	0.238	***			
dry grass 0 to 10cm layer	-0.332	***	herbaceous 40 to 50cm layer	0.200	**			

	397	for eac	h variable)	The state of the s	
Environmental Variable	рсс	sig	Environmental Variable	рсс	sig
rock	-0.106	*	annual 20 to 30cm layer	0.106	*
rubble	0.223	***	annual 140 to 150cm layer	0.105	*
refuse	0.135	**	annual 150 to 160cm layer	0.105	*
green grass 20 to 30cm layer	0.122	**	annual 160 to 170cm layer	0.105	*
green grass 30 to 40cm layer	0.177	***	herbaceous 120 to 130cm layer	-0.106	*
green grass 40 to 50cm layer	0.168	***	herbaceous 130 to 140cm layer	-0.099	*
green grass 50 to 60cm layer	0.158	**	herbaceous 140 to 150cm layer	-0.099	*
green grass 60 to 70cm layer	0.130	**	shrub 40 to 50cm layer	-0.128	* *
dry grass 0 to 10cm layer	0.122	*	shrub 50 to 60cm layer	-0.175	**
dry grass 10 to 20cm layer	0.195	***	shrub 60 to 70cm layer	-0.217	**
dry grass 20 to 30cm layer	0.177	***	shrub 70 to 80cm layer	-0.192	**
dry grass 30 to 40cm layer	0.207	***	shrub 80 to 90cm layer	-0.186	**
dry grass 40 to 50cm layer	0.183	***	shrub 90 to 100cm layer	-0.200	**
dry grass 50 to 60cm layer	0.182	***	shrub 100 to 110cm layer	-0.183	**
dry grass 60 to 70cm layer	0.172	***	shrub 110 to 120cm layer	-0.155	* 1
dry grass 70 to 80cm layer	0.144	**	shrub 120 to 130cm layer	-0.122	**
dry grass 80 to 90cm layer	0.126	*	shrub 130 to 140cm layer	-0.110	*
dry grass 90 to 100cm layer	0.118	*			

Number of Species. Garigue: WET sites (n quadrats= 200; degrees of freedom = 197 each variable)							
Environmental Variable	pec	sig	Environmental Variable	pcc	sig		
leaf litter	-0.146	*	annual 140 to 150cm layer	0.141	*		
rock	-0.168	*	annual 150 to 160cm layer	0.141	*		
rubble	0.319	***	annual 160 to 170cm layer	0.141	*		
refuse	0.170	*	herbaceous 20 to 30cm layer	0.139	*		
lichen	-0.185	**	herbaceous 30 to 40cm layer	0.161	*		
dry grass 30 to 40cm layer	0.215	**	herbaceous 40 to 50cm layer	0.157	*		
dry grass 40 to 50cm layer	0.205	**	shrub 0 to 10cm layer	-0.264	***		
dry grass 50 to 60cm layer	0.191	**	shrub 10 to 20cm layer	-0.256	aje aje a		
dry grass 60 to 70cm layer	0.157	**	shrub 20 to 30cm layer	-0.241	***		
dry grass 0 to 10cm layer	0.290	***	shrub 30 to 40cm layer	-0.212	**		
dry grass 10 to 20cm layer	0.374	***	shrub 40 to 50cm layer	-0.221	**		
dry grass 20 to 30cm layer	0.308	***	shrub 50 to 60cm layer	-0.240	***		
dry grass 30 to 40cm layer	0.292	***	shrub 60 to 70cm layer	-0.232	***		
dry grass 40 to 50cm layer	0.229	**	shrub 70 to 80cm layer	-0.184	**		
dry grass 50 to 60cm layer	0.211	**	shrub 80 to 90cm layer	-0.199	**		
dry grass 60 to 70cm layer	0.212	**	shrub 90 to 100cm layer	-0.206	**		
dry grass 70 to 80cm layer	0.170	*	shrub 100 to 110cm layer	-0.171	**		

		varia	ble)		
Environmental Variable	pcc	sig	Environmental Variable	рсс	sig
logs	0.179	**	shrub 10 to 20cm layer	0.141	*
dry grass 50 to 60cm layer	0.157	*	shrub 60 to 70cm layer	-0.210	**
dry grass 80 to 90cm layer	0.172	*	shrub 70 to 80cm layer	-0.205	**
annual 50 to 60cm layer	0.188	**	shrub 80 to 90cm layer	-0.169	*
annual 60 to 70cm layer	0.151	*	shrub 90 to 100cm layer	-0.191	**
annual 70 to 80cm layer	0.150	*	shrub 100 to 110cm layer	-0.200	**
herbaceous 60 to 70cm layer	-0.142	*	shrub 110 to 120cm layer	-0.205	**
herbaceous 70 to 80cm layer	-0.140	*	shrub 120 to 130cm layer	-0.202	**
herbaceous 80 to 90cm layer	-0.158	*	shrub 130 to 140cm layer	-0.204	**
herbaceous 90 to 100cm layer	-0.181	**	shrub 140 to 150cm layer	-0.185	**
herbaceous 100 to 110cm layer	-0.194	**	shrub 150 to 160cm layer	-0.167	**
herbaceous 110 to 120cm layer	-0.165	*	shrub 160 to 170cm layer	-0.226	***
herbaceous 120 to 130cm layer	-0.155	*			

	o; degrees		dom = 1197 for each variable		
Environmental Variable	pcc	sig	Environmental Variable	рсс	sig
soil	0.062	*	annual 90 to 100cm layer	0.058	*
shingle	-0.174	***	shrub 0 to 10cm layer	-0.083	* *
stone	-0.108	***	shrub 10 to 20cm layer	-0.098	**
rock	-0.092	***	shrub 20 to 30cm layer	-0.097	**
rubble	0.129	***	shrub 30 to 40cm layer	-0.105	**
bryophytes	-0.112	***	shrub 40 to 50cm layer	-0.112	**
green grass 10 to 20cm layer	0.108	***	shrub 50 to 60cm layer	-0.111	**
green grass 20 to 30cm layer	0.079	**	shrub 60 to 70cm layer	-0.137	**
green grass 30 to 40cm layer	0.065	*	shrub 70 to 80cm layer	-0.118	**
green grass 40 to 50cm layer	0.062	*	shrub 80 to 90cm layer	-0.105	**
green grass 50 to 60cm layer	0.069	*	shrub 90 to 100cm layer	-0.104	**
annual 10 to 20cm layer	0.062	*	shrub 100 to 110cm layer	-0.086	*
annual 20 to 30cm layer	0.074	**	shrub 110 to 120cm layer	-0.075	*:
annual 30 to 40cm layer	0.066	*	shrub 120 to 130cm layer	-0.066	*
annual 40 to 50cm layer	0.078	**	shrub 130 to 140cm layer	-0.065	*
annual 50 to 60cm layer	0.100	***	shrub 140 to 150cm layer	-0.057	*
annual 60 to 70cm layer	0.110	***	shrub 150 to 160cm layer	-0.063	*
annual 70 to 80cm layer	0.089	**	tree >200cm layer	-0.060	*
annual 80 to 90cm layer	0.070	*			

Species Abundances. Sand, Steppe and Garigue combined: WET sites (n quadrats= 600; degrees of freedom = 597 for each variable)									
Environmental Variable	рсс	sig	Environmental Variable	рсс	sig				
soil	0.115	**	annual 50 to 60cm layer	0.104	pk pk				
leaf litter	0.091	*	annual 60 to 70cm layer	0.087	*				
shingle	-0.242	***	herbaceous 0 to 10cm layer	0.149	**				
stone	-0.099	*	herbaceous 10 to 20cm layer	0.142	**				
rock	-0.130	***	shrub 0 to 10cm layer	-0.234	**				
rubble	0.164	***	shrub 10 to 20cm layer	-0.231	**				
bryophytes	-0.107	**	shrub 20 to 30cm layer	-0.227	**				
lichen	-0.126	**	shrub 30 to 40cm layer	-0.213	**				
green grass 0 to 10cm layer	-0.092	*	shrub 40 to 50cm layer	-0.208	**				
green grass 10 to 20cm layer	0.110	**	shrub 50 to 60cm layer	-0.190	**				
dry grass 0 to 10cm layer	0.153	***	shrub 60 to 70cm layer	-0.176	**				
dry grass 10 to 20cm layer	0.204	***	shrub 70 to 80cm layer	-0.128	* *				
dry grass 20 to 30cm layer	0.134	***	shrub 80 to 90cm layer	-0.107	ak aj				
dry grass 30 to 40cm layer	0.087	*	shrub 90 to 100cm layer	-0.086	*				
annual 10 to 20cm layer	0.126	**	tree >200cm layer	-0.100	*				
annual 20 to 30cm layer	0.082	*							

			597 for each variable)		
Environmental Variable	рсс	sig	Environmental Variable	рсс	sig
shingle	-0.098	*	annual 70 to 80cm layer	0.109	**
stone	-0.129	**	herbaceous 0 to 10cm layer	-0.113	**
refuse	0.115	**	herbaceous 10 to 20cm layer	-0.102	* *
bryophytes	-0.131	**	herbaceous 20 to 30cm layer	-0.097	* *
green grass 0 to 10cm layer	0.144	***	herbaceous 100 to 110cm layer	-0.089	*
green grass 10 to 20cm layer	0.099	**	shrub 60 to 70cm layer	-0.097	*
green grass 20 to 30cm layer	0.133	***	shrub 70 to 80cm layer	-0.105	**
green grass 30 to 40cm layer	0.127	**	shrub 80 to 90cm layer	-0.099	*
green grass 40 to 50cm layer	0.108	**	shrub 90 to 100cm layer	-0.119	**
green grass 50 to 60cm layer	0.129	**	shrub 100 to 110cm layer	-0.118	3/c 3/c
green grass 60 to 70cm layer	0.107	**	shrub 110 to 120cm layer	-0.119	* *
dry grass 10 to 20cm layer	-0.126	**	shrub 120 to 130cm layer	-0.118	36.36
annual 30 to 40cm layer	0.109	* *	shrub 130 to 140cm layer	-0.117	* *
annual 40 to 50cm layer	0.113	**	shrub 140 to 150cm layer	-0.103	* *
annual 50 to 60cm layer	0.116	**	shrub 150 to 160cm layer	-0.093	*
annual 60 to 70cm layer	0.141	***			

Species Abundances. Sand: WET and DRY sites (n quadrats= 400; degrees of freedom = 397 for each variable)									
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig				
shingle	-0.309	***	annual 60 to 70cm layer	0.102	*				
stone	-0.140	**	herbaceous 0 to 10cm layer	0.116	*				
green grass 0 to 10cm layer	0.157	**	herbaceous 10 to 20cm layer	0.152	**				
green grass 10 to 20cm layer	0.223	***	herbaceous 20 to 30cm layer	0.105	*				
green grass 20 to 30cm layer	0.118	*	herbaceous 70 to 80cm layer	0.100	*				
green grass 50 to 60cm layer	0.127	**	tree >200cm layer	-0.205	***				
green grass 60 to 70cm layer	0.137	**							

Species Abundances. Sand: WET sites (n quadrats= 200; degrees of freedom = 197 for eac variable)									
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig				
shingle	-0.316	***	dry grass 20 to 30cm layer	0.236	***				
green grass 10 to 20cm layer	0.252	***	annual 0 to 10cm layer	0.141	*				
dry grass 0 to 10cm layer	0.366	***	herbaceous 10 to 20cm layer	0.153	sk				
dry grass 10 to 20cm layer	0.286	***	tree >200cm layer	-0.327	***				

Species Abundances. Sand: DRY sites (n quadrats= 200; degrees of freedom = 197 for each variable)									
Environmental Variable	рсс	sig	Environmental Variable	pcc	sig				
shingle	-0.236	***	green grass 20 to 30cm layer	0.165	*				
stone	-0.289	***	dry grass 10 to 20cm layer	-0.289	**:				
rock	-0.163	*	annual 10 to 20cm layer	-0.157	*				
green grass 0 to 10cm layer	0.215	**	annual 60 to 70cm layer	0.241	**:				
green grass 10 to 20cm layer	0.151	*	annual 70 to 80cm layer	0.182	**				

Species Abundances. Steppe: WET and DRY sites (n quadrats= 400; degrees of freedon 397 for each variable)								
Environmental Variable	pcc	sig	Environmental Variable	pcc	sig			
soil	-0.141	**	shrub 10 to 20cm layer	-0.108	*			
leaf litter	0.177	***	shrub 20 to 30cm layer	-0.127	* *			
rock	0.186	***	shrub 30 to 40cm layer	-0.137	* *			
rubble	0.207	***	shrub 40 to 50cm layer	-0.163	* *			
bryophytes	0.145	**	shrub 50 to 60cm layer	-0.156	* 1			
green grass 10 to 20cm layer	0.254	***	shrub 60 to 70cm layer	-0.147	ak a			
green grass 20 to 30cm layer	0.208	***	shrub 70 to 80cm layer	-0.143	ok o			
green grass 30 to 40cm layer	0.111	*	shrub 80 to 90cm layer	-0.136	nk n			
dry grass 0 to 10cm layer	-0.148	**	shrub 90 to 100cm layer	-0.132	* 1			
dry grass 60 to 70cm layer	-0.138	**	shrub 100 to 110cm layer	-0.136	*:			
dry grass 70 to 80cm layer	-0.118	*	shrub 110 to 120cm layer	-0.145	*			
dry grass 80 to 90cm layer	-0.102	*	shrub 120 to 130cm layer	-0.136	* 1			
dry grass 90 to 100cm layer	-0.099	*	shrub 130 to 140cm layer	-0.136	7¢ 1			
herbaceous 0 to 10cm layer	0.260	***	shrub 140 to 150cm layer	-0.136	* 1			
herbaceous 10 to 20cm layer	0.222	***	shrub 150 to 160cm layer	-0.136	* 1			
herbaceous 50 to 60cm layer	-0.110	*	shrub 160 to 170cm layer	-0.128	* 1			
herbaceous 60 to 70cm layer	-0.102	*	shrub 170 to 180cm layer	-0.098	*			
herbaceous 110 to 120cm layer	-0.103	*	tree 120 to 130 layer	-0.098	*			
shrub 0 to 10cm layer	-0.130	**						

Environmental Variable	pcc	sig	Environmental Variable	рсс	si
leaf litter	0.401	***	herbaceous 70 to 80cm layer	-0.196	**
shingle	-0.204	**	herbaceous 80 to 90cm layer	-0.158	*
rubble	0.201	**	herbaceous 90 to 100cm layer	-0.149	*
bryophytes	0.154	*	herbaceous 100 to 110cm layer	-0.149	*
lichen	-0.249	***	herbaceous 110 to 120cm layer	-0.188	3k 3
green grass 10 to 20cm layer	0.312	***	shrub 0 to 10cm layer	-0.313	**
green grass 20 to 30cm layer	0.170	*	shrub 10 to 20cm layer	-0.287	**
dry grass 40 to 50cm layer	-0.192	**	shrub 20 to 30cm layer	-0.313	**
dry grass 50 to 60cm layer	-0.166	*	shrub 30 to 40cm layer	-0.320	**
dry grass 60 to 70cm layer	-0.282	***	shrub 40 to 50cm layer	-0.323	**
dry grass 70 to 80cm layer	-0.305	***	shrub 50 to 60cm layer	-0.319	**
dry grass 80 to 90cm layer	-0.264	***	shrub 60 to 70cm layer	-0.321	**
dry grass 90 to 100cm layer	-0.219	**	shrub 70 to 80cm layer	-0.309	**
dry grass 100 to 110cm layer	-0.188	**	shrub 80 to 90cm layer	-0.295	**
annual 50 to 60cm layer	0.203	**	shrub 90 to 100cm layer	-0.293	**
annual 60 to 70cm layer	0.180	**	shrub 100 to 110cm layer	-0.273	**
annual 70 to 80cm layer	0.174	*	shrub 110 to 120cm layer	-0.273	**
annual 80 to 90cm layer	0.216	**	shrub 120 to 130cm layer	-0.249	**
annual 90 to 100cm layer	0.154	*	shrub 130 to 140cm layer	-0.249	**
herbaceous 0 to 10cm layer	0.199	**	shrub 140 to 150cm layer	-0.249	**
herbaceous 10 to 20cm layer	0.153	*	shrub 150 to 160cm layer	-0.249	**
herbaceous 30 to 40cm layer	-0.231	***	shrub 160 to 170cm layer	-0.249	**:
herbaceous 40 to 50cm layer	-0.236	***	shrub 170 to 180cm layer	-0.249	**
herbaceous 50 to 60cm layer	-0.228	***	shrub 180 to 190cm layer	-0.249	**:
herbaceous 60 to 70cm layer	-0.211	**	shrub 190 to 200cm layer	-0.249	**:

each variable)								
Environmental Variable	рсс	sig	Environmental Variable	рсс	sig			
soil	-0.297	***	annual 50 to 60cm layer	0.182	**			
shingle	0.218	**	annual 60 to 70cm layer	0.211	* 1			
stone	0.291	***	annual 70 to 80cm layer	0.243	**			
rock	0.387	***	annual 80 to 90cm layer	0.195	3/c 3			
rubble	0.246	***	annual 90 to 100cm layer	0.209	* 3			
refuse	0.235	***	annual 100 to 110cm layer	0.156	*			
dry grass 0 to 10cm layer	-0.248	***	herbaceous 0 to 10cm layer	0.316	**			
dry grass 10 to 20cm layer	-0.268	***	herbaceous 10 to 20cm layer	0.283	**			
dry grass 20 to 30cm layer	-0.178	**	herbaceous 20 to 30cm layer	0.239	**			
annual 0 to 10cm layer	-0.164	*	herbaceous 30 to 40cm layer	0.270	**			
annual 10 to 20cm layer	-0.157	*	herbaceous 40 to 50cm layer	0.215	3¢ 3			
annual 40 to 50cm layer	0.173	*						

Environmental Variable	рсс	sig	Environmental Variable	pcc	sig
rock	-0.137	* *	annual 20 to 30cm layer	0.129	**
rubble	0.235	***	annual 30 to 40cm layer	0.121	*
refuse	0.146	**	annual 40 to 50cm layer	0.111	*
bryophytes	-0.176	***	annual 50 to 60cm layer	0.101	*
green grass 30 to 40cm layer	0.099	*	shrub 40 to 50cm layer	-0.111	**
green grass 40 to 50cm layer	0.101	*	shrub 50 to 60cm layer	-0.138	**
green grass 50 to 60cm layer	0.113	*	shrub 60 to 70cm layer	-0.219	***
dry grass 0 to 10cm layer	0.179	***	shrub 70 to 80cm layer	-0.200	**:
dry grass 10 to 20cm layer	0.158	**	shrub 80 to 90cm layer	-0.185	**:
dry grass 30 to 40cm layer	0.123	*	shrub 90 to 100cm layer	-0.196	**:
dry grass 40 to 50cm layer	0.116	*	shrub 100 to 110cm layer	-0.170	**
dry grass 50 to 60cm layer	0.132	**	shrub 110 to 120cm layer	-0.145	**
dry grass 60 to 70cm layer	0.131	**	shrub 120 to 130cm layer	-0.123	**
dry grass 70 to 80cm layer	0.103	*	shrub 130 to 140cm layer	-0.120	**
dry grass 80 to 90cm layer	0.104	*	shrub 140 to 150cm layer	-0.106	*
annual 0 to 10cm layer	-0.116	*			

Environmental Variable	pcc	sig	Environmental Variable	рсс	sig
rubble	0.410	***	herbaceous 10 to 20cm layer	0.240	***
refuse	0.169	*	herbaceous 20 to 30cm layer	0.291	***
lichen	-0.180	**	herbaceous 30 to 40cm layer	0.292	***
green grass 0 to 10cm layer	-0.207	**	herbaceous 40 to 50cm layer	0.270	***
dry grass 0 to 10cm layer	0.246	***	herbaceous 50 to 60cm layer	0.190	**
dry grass 10 to 20cm layer	0.308	***	shrub 0 to 10cm layer	-0.275	***
dry grass 20 to 30cm layer	0.228	***	shrub 10 to 20cm layer	-0.277	***
dry grass 30 to 40cm layer	0.217	**	shrub 20 to 30cm layer	-0.262	***
dry grass 40 to 50cm layer	0.154	*	shrub 30 to 40cm layer	-0.241	***
dry grass 50 to 60cm layer	0.162	*	shrub 40 to 50cm layer	-0.249	***
dry grass 60 to 70cm layer	0.182	**	shrub 50 to 60cm layer	-0.252	***
annual 0 to 10cm layer	-0.186	**	shrub 60 to 70cm layer	-0.252	***
annual 140 to 150cm layer	0.147	*	shrub 70 to 80cm layer	-0.183	**
annual 150 to 160cm layer	0.147	*	shrub 80 to 90cm layer	-0.166	*
annual 160 to 170cm layer	0.147	*	shrub 90 to 100cm layer	-0.148	*
herbaceous 0 to 10cm layer	0.179	**			

opecies /lounaunces. Garige			quadrats= 200; degrees of freed ariable)	- 157	101
Environmental Variable	pcc	sig	Environmental Variable	рсс	sig
shingle	-0.228	***	annual 60 to 70cm layer	0.202	**
stone	-0.251	***	herbaceous 0 to 10cm layer	-0.287	**:
rock	-0.186	**	herbaceous 10 to 20cm layer	-0.278	**
logs	0.146	*	herbaceous 20 to 30cm layer	-0.218	* *
refuse	0.181	**	herbaceous 30 to 40cm layer	-0.157	*
bryophytes	-0.229	***	herbaceous 100 to 110cm layer	-0.161	*
green grass 0 to 10cm layer	0.168	*	shrub 0 to 10cm layer	0.141	*
green grass 10 to 20cm layer	0.156	*	shrub 60 to 70cm layer	-0.228	**
green grass 20 to 30cm layer	0.155	*	shrub 70 to 80cm layer	-0.235	**
green grass 30 to 40cm layer	0.155	*	shrub 80 to 90cm layer	-0.212	36.2
green grass 50 to 60cm layer	0.148	*	shrub 90 to 100cm layer	-0.245	**
green grass 80 to 90cm layer	0.159	*	shrub 100 to 110cm layer	-0.229	**
dry grass 0 to 10cm layer	0.167	*	shrub 110 to 120cm layer	-0.217	3fc 2
dry grass 40 to 50cm layer	0.151	*	shrub 120 to 130cm layer	-0.208	*:
dry grass 50 to 60cm layer	0.161	*	shrub 130 to 140cm layer	-0.209	3 C 2
dry grass 80 to 90cm layer	0.159	*	shrub 140 to 150cm layer	-0.187	3¢ ;
annual 20 to 30cm layer	0.178	*	shrub 150 to 160cm layer	-0.171	3 sje 2
annual 40 to 50cm layer	0.148	*	shrub 160 to 170cm layer	-0.198	oje s
annual 50 to 60cm layer	0.209	**			

Appendix 13. Heterogeneity (Het) and complexity (Comp) for all quadrats from all sites. The quadrats are numbered 1 to 400. Quadrat 1 is the first sampled for each of the habitat types, and Quadrat 400 the last. Quadrats 1-200 are from sites sampled in the wet period, Quadrats 201-400 are from sites sampled in the dry period. The arrangement of sites follows Table 6.1.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue
1	16	132	42	916	26	405
2	18	112	44	400	24	333
3	20	110	31	375	27	445
	36	315	13	112	22	444
4		145	23	228	27	414
5	22	104	14	109	29	382
6	7	104	16	167	14	126
7	9		27	173	26	192
8	12	103	14	173	22	178
9	11	108	14	108	22	193
10	8	105			29	151
11	6	111	15	132		
12	9	105	20	135	40	335
13	8	104	20	170	25	145
14	6	102	33	389	25	135
15	11	124	20	167	25	513
16	10	115	14	105	30	416
17	19	310	19	132	20	198
18	9	105	19	119	21	128
19	9	123	18	125	24	186
20	11	111	13	111	20	236
21	11	108	21	147	22	234
22	6	103	19	156	41	533
23	7	183	17	136	29	564
24	5	191	18	220	46	878
25	6	103	11	146	24	458
26	9	105	7	200	31	374
27	5	101	10	172	34	401
28	5	101	11	173	11	121
29	7	104	10	119	20	225
30	8	199	9	112	7	105
31	7	105	10	113	18	276
32	11	243	12	106	18	212
33	5	103	7	98	12	277
34	5	103	9	108	20	765
35	7	188	7	103	12	109
36	5	103	11	115	30	285
37	16	177	4	100	14	131
38	7	162	10	105	15	130
39	11	111	5	101	21	301
40	4	181	8	97	20	351
41	9	110	12	109	26	269
41	7	133	11	101	18	256
42	5	103	12	108	29	281
	5	103	12	103	12	118
44	6	103	14	110	25	278
45	7	104	12	110	20	514
46		158	15	122	17	324
47	9	111	15	108	15	131
48	11	150	12	103	22	326
49	10	129	12	107	19	363
50	7	102	15	109	30	278

Appendix 13: Heterogeneity and complexity for all quadrats from all sites.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue
52	7	119	11	100	32	357
53	6	103	7	102	40	468
54	7	104	13	107	32	342
55	7	104	16	105	37	322
56	8	106	22	152	21	1049
57	9	105	26	150	17	140
58	12	102	14	108	19	181
59	8	104	11	106	18	147
60	8	103	7	112	25	351
61	4	102	15	107	31	544
62	4	102	9	105	28	441
63	4	101	17	122	50	712
64	4	98	9	102	38	610
65	7	103	16	121	26	334
66	9	114	13	106	38	351
67	8	138	16	111	33	594
68	8	109	15	142	38	428
69	8	125	13	114	28	213
70	5	103	17	113	43	420
71	6	115	20	117	25	264
72	4	100	17	107	27	316
73	4	101	16	108	45	335
74	4	101	16	113	40	482
75	11	163	17	112	30	285
76	9	164	18	127	28	334
77	8	127	24	122	35	411
78	8	158	22	118	34	387
79	9	154	15	120	41	550
80	9	143	13	104	38	396
81	5	106	19	236	24	275
82	4	100	16	203	26	341
83	5	102	15	152	26	295
84	8	105	13	169	25	343
85	7	104	12	193	23	356
86	6	103	7	102	22	293
87	7	104	9	104	21	212
	8	105	8	104	20	263
88	5	103	10	106	34	470
90	7	105	11	115	25	294
	4	106	17	160	21	327
91	4	101	11	112	31	358
93	4	101	12	150	22	271
	6	103	10	124	32	422
94	5	103	12	128	23	295
95	5	102	13	151	26	506
96	5	102	9	100	27	452
97		102	12	188	29	507
98	5	102	13	197	29	431
99	5	102	12	197	29	418
100	6		10	108	32	1060
101	12	113		108	24	
102	9	121	11		21	344
103	8	130	8	104	29	168
104	5	122	9	102		553
105	7	134	7	102	29	408
106	10	141	11	110	26	923

Appendix 13: Heterogeneity and complexity for all quadrats from all sites.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue
108	5	107	11	104	21	275
109	5	107	13	108	18	140
110	5	107	11	109	20 21 32 19	165
111	8	108	8	103		272
112	9	111	10	103		416
113	10	139	12	105		272
114	10	145	11	109	24	259
115	7	107	9	101	14	283
116	5	116	11	103	12	103
117	7	104	10	107	25	161
118	9	120	12	106	20	204
119	11	116	19	112	28	297
120	9	125	16	116	31	248
121	9	109	15	182	15	148
122	5	101	15	142	15	194
123	5	101	14	186	13	157
123	10	109	14	242	19	237
124	9	112	11	120	43	619
126	6	101	15	187	18	211
127	4	101	9	109	19	182
128	10	105	8	105	18	300
128	6	102	8	97	13	127
	6	103	10	125	18	256
130	10	109	11	125	24	263
131	9	104	12	136	20	198
132		115	9	104	27	237
133	7	103	6	103	24	768
134		103	14	136	20	231
135	7	130	12	121	24	314
136	11	130	11	112	28	197
137	13	107	9	105	26	336
138	7	148	8	105	26	199
139	10	105	13	131	33	387
140	9	103	16	442	34	763
141	7	111	23	494	74	1308
142	13		22	283	81	1207
143	11	115	16	182	56	455
144	11	121	13	141	42	270
145	8	118	20	341	38	466
146	5	103	17	280	52	569
147	5	105	18	277	46	365
148	7	98	15	240	36	259
149	4		19	245	37	288
150	9	109	20	215	20	512
151	8	122	14	110	18	406
152	6	104	22	236	18	343
153	4	101	16	135	19	289
154	6	104	16	238	19	265
155	4	102	19	187	20	146
156	5	102	13	130	32	491
157	5	102	14	137	14	110
158	7	120		107	7	103
159	10	115	14		37	331
160	8	108	14	121	11	
161	10	106	14	174		262
162	10	100	15	198	21	469
163	11	109	16	207	24	331

Appendix 13: Heterogeneity and complexity for all quadrats from all sites.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue
164	10	108	20	196	30	298
165	11	109	19	176	25	350
166	11	104	31	244	41 36 23	398
167	15	164		213		964
168	14	143		211		367
169	15	133	33	231	41	407
170	14	127	38	231	48	891
171	15	126	32	178	21	182
172	18	215	22	165	21	227
173	14	140	35	200	35	322
174	16	178	20	217	22	187
175	9	108	36	233	18	237
176	9	108	13	173	23	185
177	15	229	14	188	19	188
178	12	163	14	171	35	172
179	11	157	25	244	44	272
180	14	257	13	184	27	260
181	7	106	13	140	43	494
182	7	107	16	155	41	418
183	8	108	19	164	33	327
184	6	106	16	112	43	319
185	11	121	20	204	40	255
186	10	124	18	171	33	210
187	5	101	13	137	29	135
188	14	109	12	109	46	206
189	7	106	13	144	38	263
190	7	107	11	148	39	588
191	4	101	15	120	25	130
192	6	103	18	176	23	119
193	4	101	16	165	30	184
194	6	103	17	176	16	109
195	6	102	15	130	31	201
196	8	106	13	156	40	325
197	4	101	9	195	33	157
198	5	101	11	190	27	133
199	4	100	15	198	32	138
200	4	100	18	197	17	123
201	6	172	7	101	14	127
202	3	101	15	148	17	123
203	4	102	17	109	17	114
204	3	100	9	97	23	429
205	4	102	14	117	24	356
206	4	101	20	168	23	344
207	4	102	28	648	19	239
208	4	102	10	104	17	258
209	4	102	19	117	21	334
210	3	101	13	104	29	492
210	3	100	14	98	25	382
212	4	102	18	348	24	300
	3	101	10	112	28	558
213	6	103	10	104	24	318
214	3	101	11	111	29	816
215	4	101	7	108	11	123
216	4	102	15	108	20	575
217	4	102	32	287	24	436
218	3	101	20	658	18	170

Appendix 13: Heterogeneity and complexity for all quadrats from all sites.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue	
220	9	107	18	116	13	142	
221	13	117	13	146	23	188	
222	12	114	14	122	26	281	
223	17	118	16	124	34	447	
224	14	110	16	137	34	636	
225	13	111	13	108	38	578	
226	13	111	10	123	41	330	
227	11	109	17	140	28	514	
228	17	154	13	116	33	231	
229	14	112	10	114	31	486	
230	10	104	14	261	24	141	
231	10	110	16	138	54	452	
232	18	126	11	120	24	683	
233	22	153	10	106	24	231	
234	17	172	9	127	20	281	
235	21	153	9	113	21	498	
236	15	113	15	119	40	335	
237	30	284	11	114	35	650	
238	36	243	14	131	36	261	
	19	128	15	131	36	445	
239		142	14	128	40	165	
240	16	102	9	103	15	263	
241	6		8	105	17	286	
242	7	103		114	14	195	
243	9	105	18	142	6	98	
244	7	103	17		12	161	
245	7	103	22	202	8		
246	7	103	17	113	20	167	
247	7	102	16	112		558	
248	8	104	23	247	15	140	
249	7	103	8	103		157	
250	8	104	28	132	10	425	
251	7	103	19	109	13	121	
252	7	103	29	128	12	262	
253	9	105	16	112	11	115	
254	11	107	22	139	8	109	
255	9	105	5	102	11	131	
256	7	103	34	154	13	338	
257	7	103	30	182	19	503	
258	8	104	4	101	12	184	
259	7	103	20	111	12	216	
260	9	105	6	103	14	136	
261	18	125	8	116	8	107	
262	27	159	7	102	14	264	
263	26	253	9	105	12	139	
264	24	126	14	99	15	215	
265	14	174	14	117	17	250	
266	19	147	13	191	18	167	
267	22	120	13	152	18	199	
268	19	127	13	142	13	131	
269	21	160	12	151	16	206	
270	12	115	10	115	13	121	
271	20	177	13	137	15	123	
272	17	115	8	103	17	212	
273	22	121	15	115	16	145	
274	12	109	11	115	13	118	
275	12	126	15	133	13	144	

Appendix 13: Heterogeneity and complexity for all quadrats from all sites.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue
276	32	142	10	104	18	733
277	17	191	9	106	22	371
278	15	111	8	104	2	101
279	16	112	7	105	16	158
280	13	113	5	103	15	327
281	10	118	9	107	22	148
282	10	118	10	107	17	148
283	12	119	10	112	20	150
284	10	118	13	130	17	124
285	10	114	23	169	17	189
286	13	118	13	129	22	168
287	10	117	14	121	17	155
288	11	110	- 18	139	18	121
289	10	112	30	141	15	114
290	16	118	26	135	18	205
291	11	114	12	115	28	417
292	8	103	13	115	16	117
293	10	109	12	125	18	169
294	11	114	11	117	14	157
295	11	109	14	109	14	150
296	11	110	9	122	15	146
297	8	107	18	135	23	95
298	7	98	15	113	9	106
299	8	104	14	110	16	116
300	10	109	13	109	13	109
301	11	134	17	115	18	187
302	12	140	14	109	29	407
303	16	178	17	117	26	519
304	13	131	14	118	25	230
305	14	128	12	111	25	258
306	12	116	22	132	13	273
307	13	117	21	117	36	458
308	5	107	22	128	19	187
309	10	114	13	119	22	196
310	12	110	20	125	20	150
311	13	112	20	123	29	408
312	7	99	15	118	33	274
313	7	103	14	107	15	188
314	9	120	17	116	27	328
315	11	108	14	110	25	203
316	8	105	19	120	28	276
317	8	105	25	155	20	261
318	5	102	27	170	19	328
319	5	102	21	127	18	264
320	8	109	23	141	23	393
321	10	154	16	178	23	290
322	10	137	11	139	26	263
323	10	128	12	126	28	247
324	9	108	9	105	28	304
325	9	108	8	113	25	193
326	10	108	10	118	29	243
327	10	127	13	117	12	124
328	10	108	8	105	19	173
329	13	140	9	103	17	128
330	7	102	11	106	35	386
331	18	120	11	116	16	236

Appendix 13: Heterogeneity and complexity for all quadrats from all sites.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue
332	12	116	9	106	25	240
333	9	138	9	105	22	241
334	12	110	12	126	21	431
335	12	119	11	115	19	246
336	18	160	20	425	17	206
337	13	120	10	115	24	352
338	15	117	11	160	23	320
339	14	126	15	188	21	321
340	19	164	8	107	26	158
341		111	25	620	18	207
342		103	21	609	35	478
333 9 334 12 335 12 336 18 337 13 338 15 339 14 340 19 341 7 342 6 343 6		103	14	278	28	310
344	6	103	24	146	25	281
345	7	107	19	281	21	427
346	6	107	25	267	26	433
347	5	102	14	130	20	195
348	5	97	20	187	23	207
349	13	126	21	257	19	207
350	6	103	24	265	21	321
351	6	103	29	244	13	106
352	8	112	18	120	7	103
	7	104	11	110	25	
353			10	111	19	409
354	8	108	11	112	29	151
355	6		18	152	32	369
356	9	109				167
357	5	101	15	174	18	249
358	6	102	25	171	20	148
359	5	101	15	121	37	398
360	7	99	13	113	27	289
361	10	127	14	222	37	349
362	4	102	31	286	21	251
363	9	115	36	260	14	182
364	7	146	27	249	46	306
365	6	112	28	187	13	127
366	10	124	26	176	21	184
367	6	104	19	215	32	561
368	10	109	24	160	18	264
369	7	112	13	151	28	256
370	8	131	12	140	22	502
371	10	127	18	166	35	346
372	11	124	19	151	28	234
373	10	111	19	155	27	326
374	12	125	19	146	21	315
375	10	118	15	120	10	202
376	13	120	26	228	14	128
377	9	108	23	266	17	154
378	9	118	19	202	25	320
379	6	102	15	191	20	256
380	6	102	16	177	18	315
381	14	162	16	237	25	418
382	16	145	21	270	24	437
383	19	173	17	170	28	415
384	9	120	21	154	14	113
385	17	126	20	186	25	355
386	12	122	9	102	25	159
387	17	137	14	136	18	136

Appendix 13: Heterogeneity and complexity for all quadrats from all sites.

Quadrat	Het: Sand	Comp: Sand	Het: Steppe	Comp: Steppe	Het: Garigue	Comp: Garigue
388	14	119	12	126	28	431
389	8	109	15	113	20	126
390	7	107	14	117	23	162
391	9	110	15	123 162	30 20	426
392	10	132	15			175
393	8	108	14	125	13	104
394	5	106	12	105	14	119
395	7	105	105 14 135	135	15	114
396	9	113 123	17	194	47	659
397	9		15	142	37	621
398	9	110	14	133	24	176
399	6	121	11	106	24	336
400	7	109	11	106	25	437

Appendix 14. Total heterogeneity (Het) and complexity (Comp) for plots and sites. See Table 6.1 for site details.

Site	Het: plot a	Het:	Het:	Het:	Het:	Comp: plot a	Comp:	Comp:	Comp:	Comp:
S1	47	14	13	25	53	781	521	546	815	2663
S2	11	12	13	17	22	518	528	577	529	2152
S3	9	15	8	14	17	552	652	532	317	2053
S4	8	12	7	9	15	506	589	564	965	2624
S5	10	9	6	6	12	522	520	513	511	2066
S6	12	11	= 11	9	13	670	588	477	646	2381
S7	13	- 11	11	16	21	526	512	533	626	2197
S8	15	11	9	10	19	584	519	533	555	2191
S9	13	18	21	17	23	531	671	742	914	2380
S10	12	16	8	8	16	548	547	510	508	2113
S11	6	4	7	8	10	577	508	507	512	2104
S12	19	19	24	42	43	572	590	715	910	2787
S13	9	10	11	10	11	516	516	523	518	2073
S14	28	28	29	32	37	816	669	648	668	2801
S15	14	18	15	11	23	587	579	550	528	2244
S16	18	16	15	10	19	710	400	542	524	2176
S17	11	12	20	22	23	635	584	613	688	2520
S18	8	13	9	10	14	527	535	524	512	2098
S19	12	12	13	13	13	602	580	605	550	2337
S20	20	18	10	10	21	726	594	561	576	2457
S21_	67	32	45	20	72	2034	670	1003	592	4299
S22	23	15	17	14	29	804	776	528	518	2626
S23	14	15	12	29	34	512	517	504	616	2149
S24	20	20	21	25	31	547	585	556	600	2288
S25	19	13	20	16	21	978	531	675	827	3011
S26	13	15	13	22	25	527	491	521	545	2084
S27	18	16	18	15	21	902	613	603	574	2692
S28	26	21	27	20	25	1542	1183	1237	682	4644
S29	22	40	39	26	44	953	1030	973	964	3920
S30	22	21	21	21	25	775	709	767	909	3160
S31	18	31	21	48	52	572	761	604	623	3762 2626
S32	23	24	17	22	27	638	683	590	642	2570
S33	29	30	36	53	57	549	752	595	523	2419
S34	16	14	21	12	22 43	625	656	581	669	2531
S35	23	38	18	22 28	29	566	636	573	712	2487
S36	18	25	22	31	33	660	757	567	995	2979
S37	17	20	13	28	42	1860	1124	692	731	4407
S38	37	28	30	26	40	1185	842	735	1064	3826
S39	40	27	18	19	26	1022	505	660	651	2838
S40	26	15	50	37	53	2041	1070	1238	1154	5503
S41	34	41	27	33	53	2697	1226	1657	1189	6769
S42	52	37	47	29	43	1207	1633	1770	1877	6487
S43	39	27	47	56	67	2631	2006	1678	2088	8403
S44	53	60	35	38	41	1610	1542	1673	2310	7135
S45	31	34	33	34	47	2533	2778	1507	988	7806
S46	38	38	38	42	58	1345	1072	1697	1422	5536
S47	42	23	27	37	87	4001	1941	1815	1146	8903
S48	85	66	40	54	84	1710	2482	1175	1077	6444
S49	30	60	38	41	60	1815	1462	728	848	4853
S50	56	54	35	33	47	1098	1611	2213	1441	6363
S51	26	32	56	56	68	2125	1694	1993	1867	7679
S52	49	45 24	22	32	44	1018	1447	738	1362	4565

Appendix 14: Heterogeneity and complexity for all plots and sites.

Appendix 14 (continued).

Site	Het: plot a	Het: plot b	Het: plot c	Het: plot d	Het:	Comp: plot a	Comp: plot b	Comp: plot c	Comp: plot d	Comp:
S54	25	23	24	31	33	976	747	727	1781	4221
S55	24	27	35	26	43	762	765	1040	632	3121
S56	38	38	28	31	45	1601	1264	1069	1522	5791
S57	39	38	26	28	49	1354	1050	1374	1361	5132
S58	37	34	37	42	49	1695	1382	1138	1301	5619
S59	50	52	45	42	62	1206	1717	1428	1173	5527
S60	35	-33	34	49	52	1790	1044	938	2239	6006

Alpha diversity (α) (also called local diversity). The diversity of specified units such as a plot, sample or site (Lincoln *et al.*, 1998; Mag 2004).

Beta diversity (β) (also called differentiation diversity). The spatial turno change in the identities of species. A measure of the difference in scomposition either between two or more local assemblages or between local assemblages (Koleff *et al.*, 2003; Magurran, 2004).

Complexity The absolute amount of individual habitat structure composition (i.e. types of structure such as rocks, logs and vegetation) (McCoy and 1991).

Dissection sampling (Introduced in this study). The systematic and tho search for molluscs on vegetation and under rocks and other ground features, as well as the recording of the environmental variables, in quadrat **Distribution** The geographical range of a taxon or group (Krebs, 1985; Li et al., 1998).

Diversity A measure of the number of species (species richness) and relative abundance in a defined unit of study (Hurlbert, 1971; Lincoln 1998; Magurran, 2004).

Dry period From the end of May to September (Blondel and Aronson, 1 Font Tullot, 2000; Aviad *et al.*, 2004).

Endemism Native to, and restricted to, a particular geographical region (Futuyma, 1986; Lincoln et al., 1998).

Environmental variable Any variable that is measured for its possible effects on the numbers, abundances and distributions of species at sites (Lepš and Šmilauer, 2003).

Extent The total length, area or volume that exists or is observed or analyzed (Scheiner et al., 2000; Dungan et al., 2002; Fleishman et al., 2003).

Focus the scale at which the grains are aggregated. Equal to or larger than the grain size (Scheiner et al. 2000).

Gamma (γ) diversity (also called regional diversity). The diversity across a range of habitats within a geographical area or in widely separated areas, landscape or region (Rosenzweig, 1995; Magurran, 2004).

Grain The size of the elementary sampling unit (Legendre and Legendre, 1998; Fleishman *et al.*, 2003) and the standardized unit to which all data are adjusted via interpolation or extrapolation techniques, if necessary, before analysis (Scheiner *et al.*, 2000).

Habitat The locality, site and particular type of local environment occupied by an organism (Safriel and Ben-Eliahu, 1991; Lincoln *et al.*, 1998). In this study these were classified into habitat types (sand, steppe and garigue).

Habitat diversity Variations in habitat characteristics within and among habitats based on the number and amount (per unit area or per unit volume) of different structural components (i.e. types of structure such as rocks, logs and vegetation) (McCoy and Bell, 1991; Hart and Horwitz, 1991).

Habitat structure The physical structures in space which support plant and animal communities (McCoy and Bell, 1991).

Heterogeneity The number (or quantity) of habitat structure components (i.e. types of structure such as rocks, logs and vegetation) (McCoy and Bell, 1991).

Niche The organism's or species' place in the community, incorporating tolerances to physical factors, and interactions with other organisms. The fundamental niche is the entire multidimensional space that represents the total range of conditions within which an organism or species can function and which it could occupy in the absence of competitors or other interacting species; the realized niche is that part of the fundamental niche actually occupied by an organism or species (Hutchinson, 1965; Giller, 1984; Athur, 1987; Lincoln et al., 1998).

Phylogeography The spatial analysis of gene lineages within and among closely related species (Lydeard and Lindberg, 2003).

Principal structure (Introduced in this study). Habitat components, or structures, such as rock, litter, and logs, that may be important in affecting number of species and abundances.

Quadrat A delimited area for sampling flora, fauna or environmental variables. In this study the area is 1m². Also used to describe the sampling frame itself (Oekland, 1929; Brower et al., 1989; Lincoln et al., 1998).

Site Place or position where sampling is carried out, used interchangeably with location (Sutherland, 1996; Lincoln *et al.*, 1998).

Vicariance The existence of closely related taxa or biota in different geographical areas, which have been separated by natural barriers (Futuyma, 1986; Lincoln et al., 1998).

Wet period From October to the end of May (Blondel and Aronson, 1999; Font Tullot, 2000; Aviad et al., 2004).