FROM LANDSCAPE TO HOST-PLANT SCALES: BOTTOM-UP HETEROGENEITY AFFECTS INVERTEBRATE DIVERSITY AND INTERACTIONS

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SUMMARY

The influence of ecological heterogeneity on invertebrate diversity, trophic guild structure, and host-parasitoid interactions was assessed at landscape, habitat and host-plant scales. Variation in the cover of forest and spatial heterogeneity of six landscapes affected the diversity of epigeal beetles and soil fauna, indicating human land-use can structure communities that operate at fine spatial scales. Invertebrate taxon identity determined if species richness, abundance or both were affected by landscape structure; and whether the relationship was linear or hump-shaped. Above-ground diversity positively correlated with soil fauna diversity, but worm and collembola diversity correlated with different plant functional groups. Using the presence of cattle grazing in birch woodlands the impact of disturbance to semi-natural habitat on invertebrate diversity and trophic interactions was studied. Grazing led to a reduction in the height of understorey vegetation, and concomitant increase in plant diversity. This grazing-dependent habitat heterogeneity was correlated with a decline in the diversity of generalist secondary consumers but left herbivores unaffected. A host-parasitoid interaction was affected by the presence of cattle in birch woods. Increased floral diversity in the grazed sward indirectly (via increases in host density) and directly increased parasitism rates, a rare example of a tertiary trophic level being positively affected by anthropogenic disturbance. Using this host-parasitoid system we examined the influence of habitat patch size and isolation on this antagonistic interaction. The largest patches supported the greatest herbivore densities, but the parasitoid was unaffected. This differential impact of habitat structure meant that parasitism was inversely density-dependent and the potential stability of the interaction ($CV^2 > 1$) was reduced, providing a refuge from parasitism for the host. Bottom-up sources of heterogeneity at different scales affect diversity at higher trophic levels. Anthropogenic disturbance to plant communities can alter trophic guild structure and interactions between insect species.

DECLARATION

The work described in this thesis is entirely my own except for specific inputs from the people listed as coauthors in the data chapters or described in the acknowledgements. All sources of information have been acknowledged by citation. A bibliography is appended. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree. I hereby give consent for my thesis to be available for photocopying, for inter-library loan and for the title and summary to be made available to outside organisations.

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CHAPTER 1

INTRODUCTION AND THESIS OUTLINE

Ecological heterogeneity is a multifaceted term but at its core is the principle that variation at different spatial scales (e.g. global, ecosystem, landscape, habitat) in environmental constraints (biotic or abiotic) produces a response by organisms at different levels of biological organisation (individuals, populations, species, communities) (Stewart *et al.* 2000). Ecological heterogeneity is a major determinant of the distribution of biological diversity at all spatial scales (MacArthur & Wilson 1967, Hanski 1998) and can alter interactions between species (Roland & Taylor 1997, Doak 2000, Vásquez & Simberloff 2003, Vanbergen *et al.* 2006). In the modern world anthropogenic sources of ecological heterogeneity both dwarf and modify the influence of natural heterogeneity on biodiversity. A globally common form of anthropogenic disturbance to natural communities is the loss and fragmentation of forest, and the conversion of deforested land to pastoral and agricultural systems (Didham *et al.* 1998a, Davies *et al.* 2000, Driscoll & Weir 2005). This thesis examines how anthropogenic and natural ecological heterogeneity influences invertebrate diversity and community structure, how this response of invertebrate species may vary with trophic level, and how antagonistic species interactions are affected by ecological heterogeneity at habitat and host-plant scales.

These broad aims are met by utilising three spatially and biologically distinct systems. Initially the role of landscape-scale patterns in human land-use (forestry, agriculture, pastoralism) in generating patterns in the community diversity of organisms that operate at much finer spatial scales, namely epigeal (carabids) and soil-dwelling (collembola, earthworms) invertebrate species, is studied. Next, the impact of a specific anthropogenic disturbance (cattle grazing) to a semi-natural habitat (birch woodland) is considered, exploring the influence of the ecological heterogeneity arising from this habitat–scale disturbance on the diversity of different trophic guilds (secondary and tertiary consumers), and on the interaction between specialist insect herbivores and a parasitoid. Finally, an experiment is carried out to assess how heterogeneity in host-plant patches (patch size, isolation, phenology, architecture) differentially affects the abundance of a specialist herbivore, its parasitoid and parasitism rates. This thesis therefore addresses the issue of how ecological heterogeneity from landscape to host-plant scales impacts upon the diversity and interactions of invertebrate species at different trophic levels.

The literature is reviewed in Chapter 2 focussing on theoretical concepts underpinning habitat loss, fragmentation and biodiversity change, empirical evidence demonstrating how spatial heterogeneity arising from habitat loss and fragmentation may affect invertebrate species, and highlighting general trends in biodiversity losses. How the spatial structure of human–modified landscapes and habitats affect insect populations and communities is considered across a nested hierarchy of spatial scales: the landscape scale ($\geq$ 1km^2), the within fragment or habitat scale ($<$ 1km^2), and - for higher trophic levels - at the scale of the individual host-insect or host-plant species. Moreover, the impact of natural and anthropogenic heterogeneity on different trophic levels (primary and secondary consumers), and the interactions between them, is evaluated.

Chapter 3 deals with how landscape-scale patterns in habitat cover and heterogeneity arising from patterns of human land-use affects carabid beetle diversity and assemblage structure. Carabid communities were sampled in six 1km^2 landscapes in Northern Scotland that together represent a land-use intensification gradient from semi-natural forest to habitat mosaics to intensive agriculture. Carabid diversity was predicted to peak in landscapes that were a mosaic of forest and open habitats, either because the mosaic represents the intermediate point of a reduction in forest cover on this land-use gradient or because the accumulation of habitats promotes species turnover and population persistence. Whichever mechanism is operating, the habitat mosaics were predicted to support a carabid assemblage less distinct than those found in single-use landscapes, because they contain elements of both forest and agricultural species assemblages.

The same landscape scale intensification gradient is utilised in Chapter 4 to assess how habitat cover and heterogeneity produce a gradient in plant diversity and resources that influences soil fauna diversity in those landscapes. Collembola and lumbricid worms were chosen as they represent important members of the soil decomposer community and are known to be responsive to land-use and environmental gradients in the soil. It was predicted that soil collembola diversity would be highest in forested areas, declining monotonically as the landscapes became more agricultural and the litter resources decrease; while lumbricid worm diversity would show the opposite pattern as soil pH increases from agricultural inputs.

Furthermore, the prediction was tested that the collembola and lumbricid diversity would correlate with the changes along the land-use gradient to above-ground diversity of different plant functional groups.

Chapters 5 and 6 move away from the impact of landscape-scale, land-use heterogeneity on invertebrate diversity to consider how a single anthropogenic disturbance (cattle grazing) to a woodland habitat affects the trophic structure of a generalist insect assemblage and a host-parasitoid interaction. In Northern Scotland, birch woodlands represent patches of semi-natural habitat within the wider agricultural landscape. Some of these birch habitats are undisturbed by human land-use whilst others are incorporated into the predominant surrounding land-use of grazing beef cattle. The presence and absence of cattle grazing in these disjunct woodland patches represented a serendipitous experiment to test whether disturbance to a naturally fragmented habitat has a differential affect on invertebrate diversity (species richness and abundance) according to trophic level, and whether grazing can influence antagonistic interactions between insect species. Chapter 5 describes an experiment where eight marsh thistles, *Cirsium palustre*, are randomly transplanted into 10 grazed (disturbed) and 10 ungrazed (semi-natural) birch woodlands to test the hypothesis that tertiary trophic levels (predators) are more sensitive (i.e. decreased diversity and abundance) than secondary trophic levels (herbivores) to this anthropogenic disturbance. The diversity of invertebrate feeding guilds was predicted to be greater in larger and ungrazed habitat patches, and secondary consumers were expected to show a comparatively greater decrease in diversity compared with primary consumers. It was expected that these changes in trophic guild diversity would be correlated with grazing-dependent changes to vegetation diversity and structure.

Using the same birch woods system, in Chapter 6 the influence of grazing cattle in birch woodlands on a simple host-parasitoid interaction is evaluated. In Northern Scotland, *C. palustre* is attacked by the tephritid seed herbivores *Tephritis conura* and *Xyphosia miliaria,* which are in turn parasitized by the hymenopteran parasitoid *Pteromalus elevatus*. It was hypothesised that cattle would act as ecosystem engineers producing habitat heterogeneity that would directly and indirectly (trophic cascade) influence parasitism rates. The presence of grazing cattle was predicted to produce both a greater density and even dispersion of thistle host-plants, and increased plant diversity in the wider plant assemblage. Moreover, these changes to the host-plant and habitat were predicted to result in a bottom-up cascade with an increase in seed herbivore numbers and density-dependent parasitism a consequence of this anthropogenic habitat perturbation.

Pursuing the idea that a species sensitivity to habitat heterogeneity is dependent on trophic position, the tri-trophic system (identified in Chapter 6; *C. palustre* thistles, the seed herbivore *T. conura* and the parasitoid *P. elevatus*) is used in Chapter 7 to explore whether habitat patch size, patch isolation and host-plant heterogeneity differentially affect herbivore and parasitoid densities, and thus influence parasitism rates. An experiment with 240 second-year *C. palustre* thistles transplanted in 24 blocks was replicated in two sites to create a range of habitat patch sizes (2,4,8,16 individual plants) at increasing distance (10, 20, 40m) from a pre-existing source population of thistles and associated insects. The experimental *C. palustre* patches, therefore, established a gradient in larval resources (*C. palustre* seeds, *T. conura* larvae) for the dispersing seed herbivore *T. conura* and its parasitoid *P. elevatus*. Coincident with peak insect oviposition the architecture and the phenological stage of each host-plant were measured. It was predicted, firstly, that habitat patch size and isolation would differentially affect patch colonisation by the host and parasitoid and thus affect parasitism rates. Secondly that host-plant heterogeneity would both indirectly (via host insect density) and directly affect the parasitoid densities and the parasitism rate.

Finally, the results of these separate studies on invertebrate diversity and trophic interactions are broadly discussed in Chapter 8 within the context of ecological heterogeneity operating at different spatial scales. Key findings from the research are used to highlight the potential for human activities to affect diversity and species interactions, and to suggest further avenues of research.

CHAPTER 2

LITERATURE REVIEW: THE CONSEQUENCES OF ANTHROPOGENIC HABITAT FRAGMENTATION AND INTENSIFICATION FOR INVERTEBRATE ASSEMBLAGES AT DIFFERENT SPATIAL SCALES

2.1 Introduction

Human activities that pervade and disturb natural communities of plants and animals range from the fragmentation and clearance of forests (and other climax vegetation) for conversion to agriculture, to agricultural intensification, to eutrophication and pollution of terrestrial and freshwater habitats, and to land urbanisation. These anthropogenic effects will vary according to the species, population or community in question, and the severity, scale and speed of the environmental perturbation (Wilson 1988; Cappuccino & Martin 1997; Davies & Margules 1998; Golden & Crist 1999; Collinge 2000; Steffan-Dewenter *et al.* 2002; Kruess 2003; Thies *et al.* 2003). In general, the loss, fragmentation or pollution of the natural environment leads to biological impoverishment, the denuding of ecosystem processes and a potential loss of function (Klein 1989; Naeem *et al.* 1995; Roland & Taylor 1997; Lawton *et al.* 1998; Kruess & Tscharntke 2000; Vazquez & Simberloff 2003). Whilst it is undeniable that human activities change the environment it is not universally true that all animal and plant species suffer as a result. Many organisms benefit from the changes to the landscape or habitat, which in some cases can provide a new resource or niche space (e.g. Cappucino & Martin 1997). A caveat to this statement is that those organisms that profit from human-induced environmental changes tend to be more common generalist species; specialists tend to become more rare, and in some cases extinct (Gilbert *et al.* 1998; Golden & Crist 1999; Davies *et al.* 2000; Kruess & Tscharntke 2000). It is only relatively recently that the functional consequence of this biological impoverishment has begun to be considered (Klein 1989; Naeem *et al.* 1995; Roland & Taylor 1997; Wardle *et al.* 2001; Andresen 2003; Vazquez & Simberloff 2003; Tscharntke *et al.* 2005).

One potential change stemming from human-induced fragmentation of natural habitats is increased 'patchiness' or heterogeneity of the habitats (Didham *et al.* 1996; Didham *et al.* 1998a; Pimm & Raven 2000; Tscharntke *et al.* 2002b). This, in turn, can affect the dispersal and persistence of populations and species in the landscape (Cappuccino *et al.* 1998; Hanski 1998, 1999; Davies *et al.* 2000; Ellner *et al.* 2001; Bonsall *et al.* 2002; Benton *et al.* 2003). Ecological heterogeneity is a multifaceted term that can be defined in many ways but its underlying principle is that spatio-temporal variation in environmental constraints (biotic or abiotic) results in a differential response to the variation in these constraints by organisms (Stewart *et al.* 2000). More specifically heterogeneity can be any factor that induces variation in individual demographic rates. One such demographic effect occurs when dispersal of individuals results in members of a single population or cohort experiencing different environments, thus exposing them to spatio-temporal heterogeneity (Rees *et al.* 2000). Ecological heterogeneity may be revealed along environmental gradients that will structure biological communities according to their physiological tolerances or their behaviour (avoidance). These gradients alter the ideal distribution of organisms, creating a patchy world, and thereby affecting diversity and species coexistence (Begon *et al.* 1996). Examples include the stratification of the plant community structure with proximity to the tidal zone (Hacker & Gaines 1997), or the changes in microclimate between a forest edge and its centre (Didham 1998; Meiners & Pickett 1999; Dauber & Wolters 2004).

Heterogeneity arising from habitat fragmentation may operate in a hierarchical manner according to the spatial scale of the impact. For example, landscape heterogeneity may arise where differing land-uses create a mosaic of habitats. Conversely, a landscape managed solely for intensive agricultural production is likely to support few other habitats and result in a homogeneous landscape. Habitat-specific heterogeneity, however, could arise within this second scenario due to differences in altitude or geology that lessen the impact of agriculture and retain areas of semi-natural vegetation. Furthermore, within habitat patches organisms may experience individual–specific heterogeneity relating to the patchy distribution or variable genotype of their hosts or prey. Superimposed above this hierarchy are stochastic effects such as climate that produce further non-specific ecological heterogeneity (Rees *et al.* 2000).

Different sources and scales of ecological heterogeneity are liable to interact making the identification of individual factors governing the distribution of organisms difficult to identify. Importantly the effect of heterogeneity depends on the scale at which species experience spatial heterogeneity; for example, to a leaf-mining insect, the spatial distribution of its host plants within a habitat patch and the biochemical heterogeneity between plant individuals may be more relevant than a mosaic of wood and farmland. If the scale of the disturbance is greater than what the species can sense and respond to then the observed distribution is a response of the species to spatially distinct environments, and not a response to ecological heterogeneity. In contrast, where ecological heterogeneity does occur at a spatially relevant scale then the question is: does the ecological response differ when the 'resource' is presented either uniformly or heterogeneously (Stewart *et al.* 2000).

A point of distinction between anthropogenic and natural ecological heterogeneity is that the former operates at a magnitude and speed to which the majority of organisms are unable to respond and adapt (Wilson 1988; Pimm & Raven 2000). One mechanism by which anthropogenic heterogeneity leads to biological change is that its effects can cascade through food webs (Wardle *et al.* 1995; Jones *et al.* 1997; Fortin *et al.* 2005; Tscharntke *et al.* 2005; Vanbergen *et al.* 2006), affecting different functional groups (e.g. herbivores, detritivores, predators) in very different ways (Kruess & Tscharntke 1994; Didham *et al.* 1996; Didham *et al.* 1998b; Davies *et al.* 2000; Thies *et al.* 2003; Purtauf *et al.* 2005; Vanbergen *et al.* 2006). Grazing by livestock, for example, may - according to its intensity - modify the natural inter-relationships within and between plants and animals (Wardle *et al.* 2001; Vazquez & Simberloff 2003, 2004; Vanbergen *et al.* 2006). Grazing may also facilitate the emergence of distinct and diverse plant communities that would otherwise be excluded by a simpler community of competitive dominants (Hobbs 1996; Rambo & Faeth 1999; Fowler 2002; Pykala 2003). Such grazing–induced changes to the plant community may enhance or reduce insect diversity; either directly or indirectly (via trophic cascades) affecting populations of herbivores, predators and parasitoids differently (Gibson *et al.* 1992b; Sterling *et al.* 1992; Di Giulio *et al.* 2001; Cagnolo *et al.* 2002; Hartley *et al.* 2003; Woodcock *et al.* 2005). Disturbance (e.g. fragmentation) and subsequent ecological heterogeneity (e.g. variation in area or microclimate) may result in a loss of biodiversity (Fahrig 1997; Gilbert *et al.* 1998; Davies *et al.* 2000) with cascading effects leading to a change in food web structure (Sieving & Karr 1997; Frank *et al.* 2005; Borrvall & Ebenman 2006), and the loss or disruption of ecological processes (Klein 1989; Roland & Taylor 1997; Cappuccino *et al.* 1998; Andresen 2003; Vazquez & Simberloff 2003).

In this literature review I focus on spatial heterogeneity caused by a single anthropogenic impact: habitat loss and fragmentation. I consider how the landscape and patch structure (area, insularity, geometry and context) of human–modified ecosystems affect insect populations and communities across a nested hierarchy of spatial scales: the landscape scale ($\geq 1\text{km}^2$), the within fragment or habitat scale ($< 1\text{km}^2$), and at the scale of individual species.

In addition, I review how fragmentation and the heterogeneity that it produces affects different trophic levels (plant-herbivore-enemy) and the interactions between them.

2.2 Fragmentation and landscape structural heterogeneity in forest and agricultural ecosystems

2.2.1 Biodiversity change and fragmentation - theory

The loss and fragmentation of natural habitats such as forest contribute to global biodiversity impoverishment (Wilson 1988; Whitmore 1990; Watt *et al.* 1997b; Didham *et al.* 1998b; Lawton *et al.* 1998; Pimm & Raven 2000; Myers & Knoll 2001; Dunn 2004) and potentially threaten ecosystem processes (Klein 1989; Roland & Taylor 1997; Cappuccino *et al.* 1998; Steffan-Dewenter *et al.* 2002; Andresen 2003; Steffan-Dewenter 2003). Biodiversity losses post-fragmentation may arise as a result of physical edge effects (Davies & Margules 1998; Didham 1998) or biological processes (Sieving & Karr 1997), and may affect species differently according to their trophic position or rarity (Gilbert *et al.* 1998; Golden & Crist 1999; Davies *et al.* 2000). Since the 1960s this topic has been of both academic and applied interest to those interested in extinction and conservation biology (Diamond 1975, 1976; Gilpin & Diamond 1980, 1981; Diamond & Gilpin 1982; Gilpin & Soule 1986; Simberloff *et al.* 1992; Hanski 1999). MacArthur & Wilson's (1967) theory of island biogeography asserts that the number of species in an island of habitat is dependent on an equilibrium between distance-dependent immigration rates and area-dependent extinction rates, with the prediction that smaller, more isolated habitats will support fewer species compared with better connected, larger areas of equivalent habitat. This theory, in recognizing a spatial component to the mechanisms determining species distributions, generated a paradigm shift in the study of distribution and became a seminal principle of conservation biology (MacArthur & Wilson 1967).

Island biogeographical theory, however, requires a 'mainland' habitat in the conceptual framework that is often lacking in highly disturbed and intensively used landscapes. It was this observation that gave rise to metapopulation theory (Levin & Paine 1974; Hanski 1998, 1999; Van Nouhuys & Hanski 1999; Holyoak 2000; Weisser 2000; Ellner *et al.* 2001; Bonsall *et al.* 2002; Cronin 2004). While the development of this theory also focused on the distribution of organisms in a heterogeneous environment, and the balance between colonization and extinction, it did not assume the existence of a continuous 'mainland' habitat

(Hanski 1998). Instead, the persistence of populations within a heterogeneous environment is predicted to be a consequence of dispersal in a pattern of local extinction and re-colonisation of habitat fragments; so in a patchy environment, populations persist at a regional scale but may be absent from a given point in space and time (Hanski 1999). A second distinction between the two concepts is that island biogeographical theory focuses on the distribution of species assemblages in space whereas metapopulation theory is concerned with the distribution of individual species (Hanski 1998, 1999).

The application of these theoretical models to real-world conservation solutions has provoked a vociferous debate over the impact of habitat area and fragment insularity on biodiversity with particular reference to the design of biodiversity reserves (e.g. SLOSS debate) and how best to mitigate biodiversity loss (Diamond 1975, 1976; Gilpin & Diamond 1980, 1981; Diamond & Gilpin 1982; Gilpin & Soule 1986; Simberloff *et al.* 1992; Hanski 1999; Tscharntke *et al.* 2002a). Much of the evidence underpinning this debate on population persistence and extinction in fragmented landscapes is derived from conceptual modelling (Gilpin & Diamond 1981; Gilpin & Soule 1986; Kareiva & Wennergren 1995; Fahrig 1997) while empirical evidence supporting or refuting the theory is sparse or lacking (Tscharntke *et al.* 2002b; Tscharntke & Brandl 2004). In this section I review the current empirical evidence underpinning the debate over habitat loss and fragmentation and its relationship to biodiversity loss, population persistence and damage to ecosystem processes.

The effect of fragmentation on biological populations and communities is dependent on three main factors: the amount of habitat lost, the state of the remaining habitat (fragment geometry, isolation, size) and landscape context (the matrix in which the remnant patch is situated)(Kareiva 1987; Kareiva & Wennergren 1995; Fahrig 1997; Harrison & Bruna 1999). Fragmentation can effect populations and communities either physically or biologically (Didham *et al.* 1996; Didham 1998; Didham *et al.* 1998a; Harrison & Bruna 1999; Dauber & Wolters 2004); the impact will vary with the scale of the disturbance and the species in question (Tscharntke *et al.* 2002a).

The effect of habitat fragmentation on invertebrate communities varies greatly according to species and trophic level. For example, predatory species are often more sensitive to the effects of habitat fragmentation (Gilbert *et al.* 1998; Golden & Crist 1999; Davies *et al.* 2000; Tscharntke *et al.* 2002a; Thies *et al.* 2003) and according to which facet of fragmentation (e.g. loss of area, increased isolation) is important to that species (Kruess & Tscharntke 1994;

Didham *et al.* 1998a; Collinge 2000; Kruess & Tscharntke 2000). This makes the extraction of general patterns from the available empirical data difficult. Nevertheless, it seems the probability of extinction may increase with the rarity of a species. Theory and empirical studies predict that small, rare populations are more vulnerable to extinction (from factors such as environmental and demographic stochasticity), especially when isolated in habitat fragments (MacArthur & Wilson 1967; Gilbert *et al.* 1998; Hanski 1998; Golden & Crist 1999; Davies *et al.* 2000; Komonen *et al.* 2000). Some studies, however, have found the opposite effect, with rare species able to persist better in a fragmented landscape than common abundant species (Didham *et al.* 1998a), and being unaffected by isolation of habitat fragments (Collinge 2000).

2.2.2 Loss of habitat area, habitat insularity, species and population decline

Both island biogeographical and metapopulation theories predict that the isolation of a habitat patch is integral to an area's colonization potential and capacity to support persistent populations (MacArthur & Wilson 1967; Hanski 1999). The application of these theoretical concepts to nature reserve design (e.g. Diamond 1975; Gilpin & Soule 1986) together with spatially explicit modelling - centred on the spatial configuration of habitats and the mitigation of biodiversity loss (Kareiva & Wennergren 1995; Fahrig 1997) - have contributed to the debate, in the face of widespread global habitat loss and extinction (Pimm & Raven 2000), over whether area effects per se (loss of habitat) or fragmentation effects (e.g. isolation) were more important to the persistence of populations. There is, nonetheless, a paucity of empirical data relating to this debate (Tscharntke & Brandl 2004) and existing data are variable as organisms differ in their sensitivity to isolation, or because of the inherent practical difficulties of separating area and fragmentation effects from each other in replicated landscape-scale experiments. As an exception, an elegant study using a moss-microarthropod microcosm showed that gamma-diversity was elevated and population persistence improved by increasing the connectivity between habitat patches (Gilbert *et al.* 1998; Gonzalez *et al.* 1998). At the higher spatial scale of forest fragments it has also been shown that habitat corridors do facilitate movement in a number of plant and animal taxa, however this was not consistent for all the taxa surveyed and while suggestive, the presence of the taxa in the corridors does not unequivocally support the idea that increasing connectivity promotes population persistence in fragmented landscapes (Haddad *et al.* 2003). Studies on the efficacy of parasitoids in regulating insect herbivore populations have in some cases shown them to be negatively affected by habitat isolation (Kruess & Tscharntke 1994, 2000; Kruess 2003).

The majority of studies have found that the potentially negative effect of isolation on invertebrate populations and species is weak or lacking. Collinge (2000) found that improving connectivity in an experimentally fragmented grassland system did not mitigate species loss or promote re-colonisation and persistence in patches. In other cases, host-specific insect species (curculionid weevils, cicadellid leafhoppers and Lepidoptera) have been shown to be insensitive to the effects of isolation (Jonsen & Fahrig 1997; Haddad *et al.* 2003). Similarly, a study on carabid beetles in a fragmented eucalypt forest in Australia revealed no decline in species richness between continuous forest and fragments of variable size after years of isolation (Davies & Margules 1998; Davies *et al.* 2000). Different carabid species did, however, exhibit the whole range of population responses to fragmentation from declining to unaffected or increasing in density. Of the eight species studied, two were truly isolated populations (i.e. unable to disperse across non-forest area) and showed a significant decline in density (Davies & Margules 1998).

Other studies have demonstrated that area is the most important fragmentation variable to consider; in a study of leaf litter beetle species in Amazonian forest fragments, the majority of species were adversely affected by the loss of habitat area: densities declined in smaller fragments and fragment size was a significant predictor of extinction (Didham *et al.* 1998). In the same study system, dung beetle and euglossine bee density and species richness was lower in fragments compared to nearby, continuous forest (Klein 1989; Didham *et al.* 1996; Andresen 2003). It was also observed that secondary forest growth eased the effect of fragmentation on dung beetles (Klein 1989). Unfortunately this latter study did not explicitly separate the effects of habitat area from isolation. In a study that used mesocosms to separate experimentally area from isolation effects, habitat area was found to be the most important factor governing the distribution of species (Collinge 2000). Recent work, using invertebrate tri-trophic systems in an agricultural mosaic, has shown that the amount of non-crop area in the landscape affects the abundance of herbivores and parasitoids (Kruess 2003; Thies *et al.* 2003). Similarly, the abundance and diversity of solitary and social bee species was found to increase with increasing area of semi-natural fragments (Steffan-Dewenter *et al.* 2002). As well as affecting the distribution of species, the amount of habitat area can influence species interactions. Parasitoid attack on herbivore populations has been shown to vary according to the proportion of forested land (or other non-crop habitat) in a fragmented landscape (Roland & Taylor 1997; Kruess 2003; Thies *et al.* 2003). The impact of generalist predators on aphid populations was found to be enhanced by greater amounts of non-crop and perennial crops in the landscape as these areas acted as refuges from disturbance (Ostman *et al.* 2001).

2.2.3 Spatial–scale, species and trophic level

A common theme in the literature on habitat fragmentation and the spatial heterogeneity it creates at the landscape scale is that while certain generalisations can be made, for example, habitat loss and isolation leads to population declines and extinction (Pimm & Raven 2000; Gibbs & Stanton 2001), we must expect species-specific responses that do not conform to the overall trends (Kareiva 1987; Cappuccino & Martin 1997; Davies & Margules 1998; Didham *et al.* 1998a). These exceptions can lead to other generalisations on the effect of habitat fragmentation on organisms. Such species-specific variations as described above, for example, tend to arise where a species does not perceive the habitat fragmentation because dispersal or foraging occurs over a geographic range greater than that at which the disturbance impacts. This scale-dependent perception tends to happen with highly dispersive or generalist species, or because of the species trophic level.

Carabid species response to an experimentally fragmented forest is dependent on their ability to disperse between fragments and utilise the non-forest matrix (Davies & Margules 1998; Davies *et al.* 2000). Populations of species that were unable to cross or use the matrix declined, while those that were able to disperse into and use the matrix were insensitive to the effect of fragmentation (Davies & Margules 1998; Davies *et al.* 2000). Similarly, other researchers have found that curculionid weevils and cicadellid leafhoppers were unaffected by the level of isolation of habitat patches, with both generalist and specialist insect herbivores being unaffected by fragment isolation if they were able to disperse across the matrix (Jonsen & Fahrig 1997). In an experimentally fragmented goldenrod (*Solidago canadensis* L.) field the species richness of sap-sucking herbivores and parasitoid abundance declined in progressively fragmented habitat while leaf-chewing guilds and predators were unaffected. This differential response between guilds is believed to be due to the differences in habitat (host) specificity, lessening the probability that specialists will disperse to other patches in a fragmented system (Golden & Crist 1999).

Such guild-specific differences in the observed response to fragmentation has led to the trophic level hypothesis of Holt (1996) which predicts that plant distributions are determined mainly by available microhabitat; herbivore populations are wider ranging but ultimately limited to certain plant species/communities, while predators will have the largest ranges due to their need to exploit alternative prey patches. Consequently the population density of higher trophic levels is determined at greater spatial scales, and is less likely to persist in fragmented environments (Holt 1996).

Spatial scale has been shown to affect differentially populations of herbivores and their natural enemies with consequences for population regulation in fragmented landscapes. Thies *et al.* (2003) showed herbivory and parasitism in an agricultural mosaic to be scale-dependent. Overall, the percentage of non-crop area in the habitat negatively affected crop-attack by herbivores while positively affecting parasitism, however both primary and secondary consumers showed the strongest association with fragment area at the same spatial scale, refuting the idea that different trophic levels respond to different spatial scales. However, the slopes of regression analysis showed that parasitoid populations were more sensitive to the disturbance of the landscape structure giving some support to the trophic level hypothesis. Scale-dependent effects according to trophic position have been found in other systems, with predator-prey ratios increasing with area of habitat, demonstrating that the importance of natural enemies increases with spatial scale (Denys & Tscharntke 2002). Other studies have shown that the effects of area and isolation on insect species are scale-dependent with secondary consumers having greater impact on prey at greater spatial scales (Roland & Taylor 1997; Kruess & Tscharntke 2000; Kruess 2003) and are more likely to decline or go extinct following fragmentation (Didham *et al.* 1998b; Gilbert *et al.* 1998; Davies *et al.* 2000; Komonen *et al.* 2000).

Even within a trophic level, variation in specific ecology alters the perception of scale. Different hymenopteran pollinator guilds responded to the proportion of semi-natural habitat at different landscape scales, with eusocial bees (*Apis mellifera* L.) sensitive to habitat area at much greater spatial scales than solitary bee species (Steffan-Dewenter *et al.* 2002). Parasitism of spruce budworm by hymenopteran and tachinid parasitoids varied according to the parasitoid species and the spatial scale of fragmentation of balsam fir forest, with certain parasitoids having greater impact on budworm numbers in isolated habitat islands while others caused greater mortality in continuous areas (Cappuccino *et al.* 1998). Similar intra-guild variation was found with parasitoids attacking forest tent caterpillar (*Malacosoma disstria* Hübner). Forest structure and the spatial scale of fragmentation affected differently the ability of four dipteran parasitoid species in finding and attacking caterpillars of *M. disstria*. This variability was correlated with body size, the implication being that different sized animals foraged over different spatial scales and thus perceived the patchiness of the habitat differently (Roland & Taylor 1997).

2.2.4 Loss of diversity and ecosystem processes

The process of habitat fragmentation (loss of area and isolation of remnants) and its effects on species diversity and functional groups can lead to trophic cascades and ultimately to ecosystem processes being denuded (Naeem *et al.* 1995; Didham *et al.* 1996; Loreau *et al.* 2001). In tropical forest fragments, rates of litter decomposition are significantly reduced in small fragments (1ha) compared with larger fragments (10 & 100 ha) and continuous forest, whilst litter decomposition rates in 100 ha fragments are accelerated with proximity to the forest edge, compared to baseline levels in continuous forest edges. These edge and area effects are postulated to be the result of changes in the activity of decomposer organisms rather than direct physical edge effects (Didham 1998). Dung decomposition and removal rates were also negatively affected by fragment size due to lower densities and diversity of dung beetles (Klein 1989; Andresen 2003). These altered dung beetle communities have consequences for secondary seed dispersal, the proportion of seeds interred decreasing with beetle numbers and fragment area. Dispersal and burying by beetles has positive consequences for the seedling establishment and regeneration of certain plant species possibly by minimising the impact of rodent seed predators. It is known that rodent densities are elevated in smaller fragments, thus the interaction between dung beetle and rodent densities are likely to have profound effects on the forest composition, structure and processes (Andresen 2003). Forest fragmentation in the boreal zone follows a similar pattern of species losses, particularly with higher trophic levels failing to persist in fragmented habitat over time and this leading to a truncation of food chains and disruption of interactions (Komonen *et al.* 2000).

The regulation of herbivore populations by parasitism is yet another ecosystem process that interacts with scale and fragmentation. Decreased area of habitat and increasing insularity of habitat patches may lead to a proportionally greater decline in parasitism rate compared to losses in host density - due to the different scales at which these organisms forage and disperse (Kruess & Tscharntke 1994; Roland & Taylor 1997; Kruess 2003; Thies *et al.* 2003). This disruption to host-parasitoid interactions may - where parasitism is the main constraint on host population growth - lead to increased herbivore outbreaks in a disturbed and fragmented landscape. Fragmentation may negatively affect plant-pollinator interactions as the loss of disturbance-sensitive insect mutualists can lead to decreased plant fitness and subsequent decline in population viability. One such decline in a component of plant fitness showed that the numbers of seeds set per plant declined significantly with fragmentation, and that this was related to a two- to three-fold decrease in pollinator visitation (Didham *et al.* 1996). In an experimentally fragmented goldenrod (*S. canadensis*) system, Kareiva (1987) showed that habitat fragmentation increased the likelihood of an aphid (*Uroleucon nigrotuberculatum* Olive) outbreaking due to fragmentation interfering with the non-random searching behaviour of its predator (*Coccinella* sp.), a decoupling of a species interaction via a differential response to fragmentation leading to a loss in population regulation.

2.2.5 Summary

The fragmentation of semi-natural habitats leads to biodiversity loss via the twin processes of habitat isolation and decrease in habitat area. The relative importance of these mechanisms varies with the spatial scale of the disturbance and scale-dependent perception of that disturbance by a given species - largely a property of the trophic position or dispersal power of the species. Available evidence suggests that the fragmentation of semi-natural habitat together with scale-dependent species responses leads to the de-coupling of species interactions, with probable impacts on ecosystem processes. Despite the acknowledged importance of insects as pollinators, decomposers and consumers it is remarkable that, to date, so little data have been collected on the impact of habitat fragmentation on processes and ultimately ecosystem function. The paucity of empirical work reflects the difficulties inherent in manipulating landscape heterogeneity in order to simulate the effects of fragmentation and partly it represents a historical failure of scientists and policy makers to realise the potential functional consequences of declining biodiversity. Fortunately over the last 20 years the establishment of long-term and large-scale studies on forest fragmentation (e.g. Klein 1989, Davies & Margules 1998, Andresen 2003), together with the use of mesocosms (e.g. Gilbert *et al.* 1998, Collinge 2000, Thies *et al.* 2003) has begun to enable the elucidation of patterns and processes relating to habitat fragmentation, landscape hetereogeneity and invertebrate assemblages.

2.3 Habitat-specific heterogeneity, intensification and impacts

In causing a decline in the amount and connectivity of habitat at the landscape level human activities drive a loss of biodiversity and denude species interactions. These human impacts also extend to smaller spatial scales resulting in further losses of biodiversity and disruption to species interactions within habitats such as natural forest or grassland habitats, and their anthropogenic analogues: silvicultural and agricultural habitats. The presence and intensification of human management practices in both natural and anthropogenic habitats results in plant structural and compositional changes with concomitant effects on the associated invertebrate assemblages.

2.3.1 Disturbance and heterogeneity in grasslands

One anthropogenic driver of change in invertebrate assemblages is the type and intensity of management of grassland systems; livestock grazing, mowing and fertilisation are important in creating spatio-temporal resource heterogeneity (Gibson *et al.* 1992b; Dennis *et al.* 1998; Borges & Brown 2001; Kruess & Tscharntke 2002b). These management prescriptions may result in changes to plant communities. For example, grazing may deflect the ecological succession producing an altered version of the flora (compositional change) or in changing the physical attributes of the plant community (structural or architectural change) (Rambo & Faeth 1999; Fowler 2002). These changes to plant diversity can lead to an upward trophic cascade affecting species directly or indirectly dependent on plants, the strength of the effects varying with the taxon or functional group, and with the intensity of the disturbance (Gibson *et al.* 1992a; Di Giulio *et al.* 2001; Kruess & Tscharntke 2002a; Woodcock *et al.* 2005; Vanbergen *et al.* 2006).

That grassland management impacts on invertebrate communities has been well documented for certain invertebrate groups, although the direction of the response tends to vary with the taxon and species in question. In a recent study of heteropteran bugs in intensively and extensively mown meadows (Di Guilio *et al.* 2001), it was found that the structure of the bug community differed between the two management schemes. Community structure was more homogeneous in intensive meadows compared with extensive meadows, in extensive meadows spatial effects, for example area or aspect, were as important as the management intensity in structuring the community whilst the management prescription was the dominating influence on assemblages in intensive meadows. Furthermore, the intensive meadows were marked by the dominance of a few abundant individual species while the extensive situation showed a more even dominance structure and higher species richness (Di Guilio *et al.* 2001). Species-specific responses to cutting regime varied widely - two species increased in abundance in response to mowing, six were negatively affect by either early season cuts or increased frequency of cuts, while 16 species were unaffected (Di Guilio *et al.* 2001). Species that declined in abundance with increased management intensity did so as a consequence of their life-history making them more vulnerable; either because the frequency and timing of mowing was coincident with the juvenile stage (nymphs) or adults being poor dispersers. Species able to exploit these ephemeral environments tended to be predatory, highly dispersive and multivoltine while the insensitive species were widespread habitat generalists or polyphagous grassland herbivores (Di Guilio *et al.* 2001).

Another study (Kruess & Tscharntke 2002) examined insect community responses along a grazing intensity gradient ranging from ungrazed to intensively grazed grasslands. In general, a significant decrease in insect species richness and abundance was found with higher diversity in the ungrazed compared to intensively grazed pastures. Changes to the physical structure of the sward between ungrazed and grazed systems drove this community change. Both Lepidoptera and certain Hymenoptera guilds responded positively to increased vegetation height in ungrazed grassland, while grasshopper species diversity was significantly predicted by vegetation heterogeneity – a mosaic of bare ground and plant cover required for grasshopper oviposition and feeding needs (Kruess & Tscharntke 2002). This result is in agreement with the idea that bottom-up effects such as resource heterogeneity or productivity promote the diversity of higher trophic levels (Strong *et al.* 1984). The difference in community assembly between intensively and extensively grazed pasture was less pronounced with only a few taxa showing an increase in diversity with extensification. This was not, however, linked to bottom-up effects (i.e. increased architectural complexity or plant diversity), but instead was thought to be a direct disruption of plant-herbivore interactions by livestock. Higher trophic levels were also negatively affected by grazing with percentage parasitism by cuckoo wasps three times greater in the ungrazed situation compared with pastures (Kruess & Tscharntke 2002). This again adds support to the idea that higher trophic levels are more sensitive to disturbance (Kruess & Tscharntke 1994; Didham *et al.* 1998b; Davies *et al.* 2000; Kruess & Tscharntke 2000; Thies *et al.* 2003).

These two examples (Di Guilio *et al.* 2001; Kruess & Tscharntke, 2002), along with other studies (Gibson *et al.* 1992a; Gibson *et al.* 1992b; Sterling *et al.* 1992; Dennis *et al.* 1997; Dennis *et al.* 1998; Borges & Brown 2001), indicate that responses to grazing tend to be taxon-specific. In general, however, invertebrate populations can be divided into two categories - those that respond to plant composition and those that respond to plant architecture and habitat structure. Specialists on herbaceous plants are found to be responsive to changes in plant composition, mainly due to intimate host plant relationships, for example, leaf miners and phyotphagous Coleoptera (Sterling *et al.* 1992, Gibson *et al.* 1992a). However, grass specialists (Auchenorrhyncha) are also responsive to changes in sward structure with grazing intensity (Brown *et al.* 1992; Gibson *et al.* 1992a), as are generalists such as Heteroptera (containing a range of trophic guilds) and obligate predators such as spiders (Gibson *et al.* 1992a; Gibson *et al.* 1992b). In a study by Dennis *et al.* (1998) structural hetereogeneity produced by experimental grazing treatments supported a more diverse assemblage of small-bodied invertebrates in upland grassland; in paired plots where reduction in grazing produced greater heterogeneity (tussocks) a more diverse fauna was supported compared to structurally simpler heavily grazed plots (sward). These structural refuges also mitigated the overall trend in the experiment of declining diversity with increased grazing intensity. Similar work (Dennis *et al.* 2001) found that generally structural heterogeneity (arising from reduction in grazing) not botanical composition was more important for arachnid species composition and abundance, although certain species did prefer the intensively grazed areas. Consequently it was proposed that a mosaic of grazing pressure should be maintained in this system as a conservation measure to ensure that all species were accommodated (Dennis *et al.* 1997; Dennis *et al.* 2001). In contrast, a study of pastures under different management in the Azores by Borges and Brown (2001) found that taxa, when grouped into functional groupings (forb-feeders, grass-feeders, web-building spiders), responded not to vertical structure but to plant alpha diversity and abundance of plant functional types (e.g. forbs).

Species differ in their sensitivity to the direct and indirect effects of grazing. The above studies show differing sensitivities of higher taxonomic and functional units to habitat structure and compositional changes in plant communities. Using spatial statistics to test for association between grazing-driven landforms and aggregations of beetles, Dennis *et al.* (2002) demonstrated that carabid and staphylinid species responded differently to components of grazing impact. Some beetle species were associated with land-form, others with grazing intensity and mammalian grazer species, while others responded to microclimate changes (e.g. soil moisture and landform) (Dennis *et al.* 2002). Despite these taxon-specific changes, in general, increased intensity of grazing led to an overall decline in diversity with an impoverished or distinctive fauna in the most intensively grazed situation (Gibson *et al.* 1992a; Di Giulio *et al.* 2001; Cagnolo *et al.* 2002; Kruess & Tscharntke 2002b).

Grazing can affect the structure of invertebrate communities with the elimination of rare, specialist species and often the promotion of abundant generalists resulting in changes to the taxonomic and trophic guild structure of the community (Gibson *et al.* 1992a; Di Giulio *et al.* 2001; Cagnolo *et al.* 2002). In a study by Dennis *et al.* (1997) grazing altered beetle assemblages on upland grassland systems. Species associated with intense grazing tended to be copraphages or predators of dung-arthropods, and were widespread and common in grassland, while larger-bodied carabid species were negatively affected by intense grazing due to their need for structurally more complex vegetation (Blake *et al.* 1994). Cagnolo *et al.* (2002) found that intense grazing led to major changes to invertebrate assemblages in montane grasslands. The abundance, species richness and biomass of invertebrate families were lower in intensively grazed areas compared with lightly grazed and ungrazed areas. The heavily grazed areas were distinct in terms of the taxonomic composition of invertebrate assemblages with different assemblages being found in the most disturbed situation for both insect families and Coleoptera (Cagnolo *et al.* 2002). Functional changes accompanied this taxonomic turnover with a significant decrease in both density and biomass of predators and parasitoids in the heavily grazed areas compared to lightly grazed and ungrazed areas. This change was accompanied by changes in the relative abundance of herbivore guilds; intensively grazed grassland had an order of magnitude fewer sap-sucking insects with concomitant increase in the number of chewing herbivores (Cagnolo *et al.* 2002). These taxonomic and functional changes are postulated to be a consequence of the simplification in structure of the sward under intensive grazing pressure.

These results (Cagnolo *et al.* 2002) are consistent with the hypothesis that resource-concentration or heterogeneity is reduced by the large-scale offtake of vegetation biomass by vertebrate herbivores, with consequences for invertebrate populations. The loss of secondary consumers is consistent with studies in forest and agricultural ecosystems that demonstrate the differential impact of disturbance on insect trophic guilds (Komonen *et al.* 2000), leading to the possible erosion of ecosystem processes, such as the regulation of herbivore populations and suppression of outbreaks (Kruess & Tscharntke 1994).

2.3.2 Disturbance and heterogeneity in forests

Forest fragmentation at landscape scales has far-reaching consequences for invertebrate biodiversity (see above), however, the impact of anthropogenic heterogeneity in forest ecosystems extends to smaller spatial scales, affecting invertebrate assemblages within managed forestry and in remaining semi-natural fragments. Recent work by Vásquez and Simberloff (2003) shows that livestock grazing in forests also impacts on invertebrate assemblages. Their study was able to show that the presence of cattle disrupted plant-pollinator relationships to produce mutualist webs that were distinct from those found where cattle are absent. This effect of grazing regime on pollinator interactions was strong and outweighed the influence of geographical location (i.e. sites co-located were more similar in their interaction web structure compared to more distant sites, but the influence of grazing was significant over and above these effects (Vazquez & Simberloff 2003)). The niche breadth hypothesis predicts that the host or habitat specificity of a species determines its response to disturbance - specialist organisms are more likely to be negatively affected by habitat fragmentation and other forms of disturbance than generalists (Golden & Crist 1999; Vazquez & Simberloff 2002). Earlier work, however, in the above plant-pollinator system demonstrated that the disruption to these interaction webs in grazed forest was not a consequence of the degree of specialisation of the mutualists (Vásquez & Simberloff 2002). In fact, the difference between the grazing regimes was identified to be a consequence of the loss of a number of "keystone interactions" centred on certain numerically dominant plant and insect generalists. The loss of these key mutualist species alters the overall structure of the interaction web and is likely to cascade though the web as these important generalist species interact exclusively with rarer, specialist species in the community (Vásquez & Simberloff 2003). The possible mechanisms underpinning these grazer-mediated changes in interactions could not be separated explicitly in this observational work, although it was suggested that some of the observed interaction losses may arise because grazing directly reduces the abundance of certain plant species - so the decline in the frequency of interactions involving this plant species is a function of their increased rarity. This pattern, however, was not universal and therefore the observed changes in those species not affected directly by cattle remain likely to be via complex indirect routes (Vásquez & Simberloff 2003).

Some evidence (Wardle *et al.* 2001) that browsing by introduced ungulates (deer and goat) can impact on forest food-webs has been supplied by data from New Zealand, where historically recent introductions provide a natural experiment on how forest ecosystems respond to disturbance by novel vertebrate herbivores. Wardle *et al.* (2001) aimed to show that these introductions produced a trophic cascade impacting on components of the soil microflora and fauna, as well as on soil processes. Browsing by ungulates produced changes in the composition of the plant community and lowered vegetation density, at least in the browsed layer. Only one taxon (humus nematodes), however, was negatively affected across all sites by the magnitude of changes in plant diversity. Overall, the majority of micro-, meso– and macrofauna studied showed idiosyncratic responses to browsing-induced changes to plant communities, refuting the idea that changes in plant community diversity will cascade through food-webs in a clear and consistent manner (Wardle *et al.* 2001). There were overall reductions in the density of dominant meso– and macrofaunal groups in response to browsing, but in general, these soil faunal changes were correlated with other variables (variation in macroclimate, stand characteristics, soil nutrients) not changes to plant community diversity. Significant relationships between browsing–induced changes to leaf-litter composition and habitat diversity in the litter layer and certain invertebrate groups (nematodes, gastropods and diplopods) were found (Wardle *et al.* 2001). Browsing had some direct consequences for soil processes, both carbon and nitrogen storage in the soil showed strong browsing effects, and these had significant consequences for certain fauna (e.g Gastropoda), but again the direction of these responses was idiosyncratic (Wardle *et al.* 2001). The study by Wardle *et al.* emphasises the wide-ranging effects of vertebrate herbivores on invertebrate assemblages, but the idiosyncratic nature of the findings suggests the mechanisms via which vertebrate-induced changes operate on lower trophic levels and other food-webs are complex, difficult to disentangle, and vary with location and species.

Aside from the impact of introduced ungulate herbivores on forest invertebrates, spatial heterogeneity may arise from forestry practices, such as selective logging or clear felling, with generally negative consequences for invertebrate assemblages. Grove (2002) in a study of the saproxylic beetle fauna of a tropical rainforest in Queensland found that these assemblages were generally negatively affected by greater intensity of disturbance. Levels of beetle abundance were significantly lower in selectively logged and secondary forest compared with areas of old-growth forest. Although the effect on species richness was not as clear, there was a significant difference in mean richness between old–growth and secondary forest (Grove 2002). Ordination analysis demonstrated that the assemblages in the three forest categories were distinct from each other in terms of community composition, with the difference between the old-growth and secondary re-growth most pronounced. Furthermore, these differences may be functionally significant as the trophic guild structure of the different management areas was significantly different. Old-growth forest supported significantly more predators, detritivores and mycophages in the larval feeding guilds with the most profound changes being between the old-growth and secondary regrowth (Grove 2002). This truncation of a food–chain and loss of predators with increased disturbance is consistent with other studies (e.g. Watt *et al.* 1997b; Komonen *et al.* 2000).

In another tropical system (Watt *et al.* 1997a; Watt *et al.* 1997b) showed that management intensity of planted forest in Cameroon negatively affected a range of invertebrate orders and families in the forest canopy. Overall, invertebrates were more abundant in plots subjected to low-intensity, selective manual logging compared to complete, mechanical clearance (Watt *et al.* 1997ab). The authors tentatively suggest that due to some of the taxa sampled (Hymenoptera, Araneae) being generally predatory there may be consequences for herbivore regulation in more intensively used forests. Jones *et al.* (2003) examined termite assemblages along a gradient of increasing intensity of tropical forest management–species richness and abundance declined with increasing intensity of disturbance. Correlation with certain environmental variables (e.g. tree basal area) suggested that increasing management intensity simplified the physical structure of the habitat. These changes altered the microclimate and removed the feeding and nesting sites important to the termite fauna (Jones *et al.* 2003). Again, management intensification of forest may have ramifications for ecosystem processes; in this case, the depletion of termites may impact on forest decomposition, with concomitant impacts on other soil food–web components.

A study along a successional gradient of logged boreal forest in Finland demonstrated that there was a high level of complementarity between samples of invertebrates taken from different age classes of forest (Niemela *et al.* 1996). In the three taxa studied (ants, carabid beetles, spiders), over 50 % of the catch from any forest age class were present in other age classes, and in the mature forest. The majority of spiders and carabid species were widely distributed across all the forest age classes, while a higher proportion of ant species had a narrower range (Niemela *et al.* 1996). Nevertheless, in all three arthropod groups there were clear differences between assemblage from younger, more open age classes and mature, closed canopy classes (Niemela *et al.* 1996). When the compositional similarity of samples was compared from within the age classes it was observed that there was greater heterogeneity in the composition of the samples from younger successional classes that in samples from mature forest, and that this heterogeneity was operating at very fine spatial scales (10-15m). The authors attribute this heterogeneity not to sampling error but actual micro-site variation (litter, ground vegetation) between structurally homogeneous tree stands (Niemela *et al.* 1996). A major determinant of the diversity of these arthropod assemblages appears to be an interaction between coarse (successional stage) and fine (microsite) heterogeneity that combine to affect the diversity of the regional species pool (Niemela *et al.* 1996).

In order to minimise losses of invertebrate biodiversity, some of which are likely to have functional importance, it would be prudent to ensure that as well as maintaining landscape-scale forest diversity (area, connectivity, context) that forest habitats should be managed to promote within-habitat heterogeneity, for example, by retaining some over-mature trees within intensively managed forest which will provide a refuge for disturbance-sensitive species (e.g. saproxylic fauna; Grove 2002) and will also create microsite variability to which less sensitive species (e.g. carabids; Niemela *et al.* 1996) will respond positively.

2.3.3 Summary

Structural and compositional changes to plant communities may arise as a result of grazing by introduced ungulates or by forestry practice. These changes may in turn cascade through invertebrate food–webs, in general, with an accompanying loss of diversity with greatest losses at higher trophic levels. Species identity determines greatly the direction of the response to these anthropogenic pressures, as does the intensity of the disturbance. Commonly invertebrate communities appear to be able to adapt to moderate disturbance but radical environmental changes resulting from the application of intensive management practices tend to result in substantial biodiversity losses. Evidence is sparse at present, but there are indications that losses at these within-habitat scales are likely to have repercussions for the overall ecosystem processes (e.g. loss of mutualist pollinators, changes to soil food webs) although the mechanisms are complex and difficult to elucidate. Again, the scale at which the disturbance operates and the organism responds are of critical importance to any measures devised to mitigate loss of biodiversity and ecosystem function.

2.4 Species–specific heterogeneity

Species are rarely uniformly distributed in space and this heterogeneity may arise as a product of many different processes that are manifested as spatio-temporal heterogeneity in the physical or biological environment. Insects rarely organise themselves according to an ideal free distribution, more often the spatial distribution of insects is patchy (Begon *et al.* 1996). This patchiness may arise as a consequence of environmental variability (physical gradients) but also due to interactions with other organisms (competition or predation). One interaction that has been the subject of both theoretical and empirical study is that between parasitoid insects and their hosts. Host-parasitoid dynamics have been the focus of study as they are abundant in most terrestrial ecosystems, have economic importance as biocontrol agents, and they provide an important ecosystem function in regulating herbivorous insect populations. Additionally host-parasitoid systems, due to their relatively simple trophic structure (one host gives rise to one parasitoid individual or family), provide a useful model to test ecological and evolutionary hypotheses in resource-consumer systems (Godfray *et al.* 2000). The impact of landscape and habitat scale anthropogenic disturbance on parasitoid populations has already been reviewed above, in this section I will first focus on spatial heterogeneity arising as a result of intrinsic processes (i.e. interactions) between hosts and parasitoids, and then on the interaction between parasitism and spatial habitat heterogeneity at very fine scales.

2.4.1 Host-parasitoid systems: an example

Interactions between hosts and parasitoids have been shown to be important at driving the population oscillations of herbivorous insects (Turchin *et al.* 2003), these oscillations driven by the time-lag in the density response of parasitoid populations to increases in host popualtion densities, both populations then crash and eventually host and then parasitoid populations recover, and the cycles start again. Heterogeneity in parasitism, arising from the spatial patchiness of host populations and non-random searching of parasitoids (Godfray *et al.* 2000) has often been purported to be a structuring factor stabilising host-parasitoid temporal dynamics (Pacala *et al.* 1990; Hassell *et al.* 1991). Density-dependent and density-independent responses of parasitoids can both contribute to the regulation or stability of host populations, and the temporal stability of host-parasitoid dynamics may be dependent on the presence of environmental heterogeneity in the form of aggregation of parasitoids and hosts (Pacala *et al.* 1990; Hassell *et al.* 1991; Godfray *et al.* 2000).

This aggregation and stabilisation of host-parasitoid dynamics may arise as a result of two different mechanisms; firstly density-dependence acting on hosts (resource competition) or parasitoids (interference) (Visser *et al.* 1999; Godfray *et al.* 2000), or secondly, as a result of spatio-temporal refuges where host populations can persist during periods of intense parasitism (Reeve *et al.* 1994; Begon *et al.* 1995; Sait *et al.* 1995; Godfray *et al.* 2000). These refuges may be physical (e.g. galls), temporal (phenological asynchrony), resistant (immunological or genetic variability), life-history (overlapping host generations with long lived adults) or they may be a consequence of spatial habitat heterogeneity (Godfray *et al.* 2000 and references therein). All these refuges are stabilising and facilitate population persistence because they result in certain host individuals in the population being more susceptible than others to parasitism (Pacala *et al.* 1990; Hassell *et al.* 1991; Godfray *et al.* 2000). It is the influence of habitat heterogeneity that has had least attention in the literature.

One empirical example that demonstrates how refuges from parasitism can arise from life-history differences between predators and prey is the case of the tussock moth (*Orgyia vetusta* Bdv.) and its natural enemies (Brodmann *et al.* 1997; Harrison 1997). This species attains extremely high densities when feeding on perennial *Lupinus* spp., yet shows a highly patchy distribution despite apparently abundant and contiguous *Lupinus* habitat. To determine what limited the spatial distribution of these patchy herbivore outbreaks, studies were carried out to assess the contribution of a number of likely parameters (host-plant quality, generalist predator abundance, rates of predation, dispersal of moths and parasitism) to the spatial distribution of the moths. Differences in host-plant quality were excluded as no differences in larval performance between outbreak and non-outbreak areas were detected for any performance parameter (e.g. pupal weight, survivorship) measured (Harrison 1997). No differences between outbreak and non-outbreak areas were found in either predator abundance or rates of predation (Harrison 1997). It was the combination of the very lower dispersal abilities of the moth and parasitism by hymenopteran and dipteran parasitoids that was creating the heterogeneity in the distribution of the moth (Harrison 1997; Brodmann *et al.* 1997). Rates of parasitism and predator-prey ratios were elevated in the zone around the outbreak (Brodmann *et al.* 1997). This pattern was due to the parasitoid population 'spilling over' the edge of the prey population, a consequence of the greater rate of dispersal by enemies, but within the patch the prey population is spared from total extinction by this constant diffusive loss of a percentage of the parasitoid population (Brodmann *et al.* 1997).

The emphasis in both modelling and empirical approaches in host-parasitoid systems has tended to focus on the influence of prey density on the behaviour and parasitism rates of parasitoid populations. A relatively new question is to what extent does habitat structure (e.g. plant patch size and dispersion) influence these predator-prey interactions, especially in view of the evidence suggesting the importance of density-independent heterogeneity in parasitism (Pacala *et al.* 1990, Hassell *et al.* 1991).

Spatial modelling has shown that the interaction between parasitoid and hosts can be modelled as a series of interconnected metapopulations where overall environmental heterogeneity can mitigate the local decline or extinction of host populations by a 'rescue effect' of immigration from other populations, so the populations persist at larger spatial scales even if they decline locally as a result of intense parasitism (Reeve 1988; Hassell *et al.* 1991; Godfray *et al.* 2000). The effect of spatial habitat heterogeneity in acting as a refuge and stabilising the dynamics of host-parasitoid systems is a relatively new area of research and little has been done empirically due to the difficulty in studying parasitoid population dynamics and dispersal in the field (Jones *et al.* 1996).

Roland and Taylor's (1997) study was among the first to examine the issue of spatial heterogeneity and its effect on host-parasitoid dynamics. Using a fragmented forest system it was found that four species of parasitoid attacking *Malacosoma disstria* responded differently to host density and fragmentation of the habitat, and that these differences were related to parasitoid body size – a surrogate of dispersal ability. The largest parasitoid species showed scale dependent density-dependence at the largest scale of fragmentation, the two medium sized parasitoid species showed a responses to intermediate scale fragmentation, while parasitism by the smallest species was greatest in highly fragmented areas (Roland & Taylor 1997). There was a significant interaction between host density and forest structure on rates of parasitism by the two smallest species (*Carcelia malacosomae* Sellers and *Patelloa pachypyga* Aldrich). *C. malacosomae* responded to host density in partially-felled forest but not in contiguous forest while the reverse was true for rates of parasitism by *P. pachypyga* (Roland & Taylor 1997). This suggests that altered forest structure either acts as a barrier to, or facilitate dispersal and aggregation by different parasitoids. These species–specific correlations were dependent on body size, and therefore relating to dispersal power and the scale at which a species perceives ecological heterogeneity. This response to forest fragmentation has the potential to disrupt the stabilising effect of parasitoid aggregation on the host population. Indeed those species that are most affected by the habitat fragmentation are those that dominate in *M. disstria* populations that are in decline, thus fragmentation may extend the duration of these herbivore outbreaks (Roland & Taylor 1997).

Doak (2000), using populations of a moth (*Itame andersoni* Swett) and its hymenoptera parasitoid complex in a naturally patchy *Dryas* host plant environment, demonstrated a general absence of a density-dependent response of parasitoids to the host, but a strong influence of habitat structure in the form of patch size and isolation. The parasitoid species showed idiosyncratic responses to habitat structure - a braconid species responding negatively to increased patch area while an ichneumonid responded positively; total parasitism was greatest in the smallest habitat patches (Doak 2000). These differences are important considering all the parasitoids were using the same host in the same simple, host plant community (Doak 2000) and reflect the importance of considering spatial scale and habitat structure when assessing parasitoid - prey interactions.

In contrast to Doak (2000) other studies have found a positive response of parasitism to increasing patch size (Sheehan & Shelton 1989; Kruess & Tscharntke 2000). Sheehan and Shelton (1989) found that an aphid parasitoid, while responding to host density, also responded independently and positively to patch size – parasitoid leaving rates were significantly lower in larger habitat patches. A study of an herbivore-predator-parasitoid system (Cappuccino 1992) showed that the predator did not respond to the density of its prey, nor did the parasitoid to its prey, the predator. The density of the parasitoid was rather positively influenced by the density of the prey of its host, indicating the parasitoid finds it easier to search for the prey item (in this case galls) rather than its cryptic host (Cappuccino 1992). It is suggested that the lack of a density relationship between the prey and the predator is a product of the predator avoiding these cues, in order to avoid its parasitic enemy (Cappuccino 1992). The important point is that considered in isolation the lack of a density–dependent response may appear maladaptive, but improved understanding of system dynamics comes when a consideration of the selective pressure from other trophic levels and spatial variability in habitat structure is included.

2.4.2 Summary

Excepting the study by Roland and Taylor (1997), the majority of the studies cited above are concerned with natural heterogeneity arising either as a result of intrinsic processes (e.g. density-dependence) that generate population structure or due to fine–grain habitat heterogeneity (e.g. plant dispersion). A few other studies have looked at how the interaction of host and parasitoid is affected by coarse-grain heterogeneity caused by human activities in the landscape (reviewed in detail above: Kruess & Tscharntke 1994, 2000; Kruess 2003; Thies *et al.* 2003). The spatial scale at which species respond to disturbance to habitat structure (fine and coarse grain) varies both between parasitoid species, and between parasitoid and host. Additionally, density–dependent regulation of host–parasitoid systems is likely to vary with this heterogeneity. These points are likely to be key to understanding the consequences of habitat fragmentation not only for host-parasitoid dynamics but also, perhaps, for other species interactions (e.g. mutualisms). Increased understanding of how spatial processes affect species interactions aswell as diversity may provide insights of practical use when managing the landscape for biodiversity conservation and maintenance of ecosystem processes.

2.5 Conclusions

The fragmentation of semi-natural habitats leads to biodiversity loss via the twin processes of habitat isolation and decrease in habitat area. The relative importance of these mechanisms varies with the spatial scale and intensity of the disturbance, and the scale-dependent perception of that disturbance by a given species (often a property of a species trophic level). Available evidence suggests that the fragmentation of habitat and subsequent intensification of land-use, together with scale-dependent species responses leads to the de-coupling of species interactions (e.g. changes to density-dependent responses of predator to prey, loss of mutualisms), the effects of which may cascade through food-webs. Such changes to food–web structure are likely to have profound impacts on ecosystem processes (e.g. decomposition, regulation). Future research must, while continuing to address the loss of numbers of individuals and species, focus on how habitat fragmentation and anthropogenic intensification affect interactions and other community dynamics either directly (e.g. changes to habitat structure) or indirectly (disruption of interactions leading to trophic cascades).

CHAPTER 3

EFFECT OF LAND-USE HETEROGENEITY ON CARABID COMMUNITIES AT THE LANDSCAPE SCALE[a]

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Carabid beetle assemblages were studied to assess how diversity and community structure varied along a gradient of land-use. This gradient was composed of six 1km^2 quadrats with an increasing proportion of agricultural land reflecting the anthropogenic fragmentation and intensification of landscapes. Carabid species richness and abundance was predicted to peak in the most heterogeneous landscape, in accord with the intermediate disturbance hypothesis (IDH), and then decline as agricultural intensification increased. It was also predicted that the different landscapes would support beetle communities distinct from each other. The IDH was unsupported - in both years of this study carabid species richness and abundance was greatest in the most intensively managed, agricultural sites. Detrended correspondence analysis revealed a clear separation in beetle community structure between forested and open habitats, and between different forest types. Canonical correspondence analysis revealed a significant correlation between beetle community structure and the environment, showing distinct beetle assemblages to be significantly associated with specific edaphic and botanical features of the land-use gradient. This study adds to increasing evidence that landscape–scale patterns in land-use significantly affect beetle community structure producing distinct assemblages.

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3.1 Introduction

A major contributing factor to the global loss in biodiversity is anthropogenic impacts in the environment, with land-use change being acknowledged as one of the more significant drivers (Myers & Knoll 2001; Novacek & Cleland 2001). The fragmentation of forest habitat and subsequent replacement by agriculture is one such land-use transition. This anthropogenic succession can, according to its intensity, result in landscapes of varying heterogeneity with impacts on the biological communities therein (Davies & Margules 1998). In Europe, much of the semi-natural forest has already been modified or replaced by agricultural or silvicultural systems managed at a range of intensities. To what extent do these different forms and intensity of land-use contribute to current levels of biodiversity? How can landscape managers halt species loss and promote sustainable biological communities? These are not trivial questions and, given recent international commitments to slow and halt biodiversity losses (e.g. Anon 2001, Anon 2002a), are politically sensitive and require urgent consideration.

This study is situated within a research framework that aims to explore how the fragmentation of semi-natural terrestrial communities and intensification of land-use impacts on biodiversity (Anon 2003). The term biodiversity has many meanings relating to different scales of biological organisation from genes to ecosystems. As such it is important that it is explicitly defined: in this project it is used to denote variation in the species composition of plant and animal communities, within the context of six landscape scenarios that constitute a gradient of increasing landscape-scale disturbance. Environmental gradients can be used to assess the impact of human activities on biological systems, and despite the complication of multiple cause-effect relationships the use of gradients may enable generalisations to be drawn from community responses to perturbation (McDonnell & Pickett 1990; Desender & Maelfait 1999; Ribera *et al.* 2001; Koivula *et al.* 2002; Niemela *et al.* 2002).

Fragmented forest-agriculture landscapes are predicted to be high in biodiversity for two reasons. Firstly, the dynamic relationship between biodiversity and disturbance is dependent on the frequency and duration of disturbance; at intermediate levels of disturbance it is proposed that competitive dominants are suppressed, facilitating colonisation by less-competitive organisms and promoting species coexistence (Connell 1978). Following this hypothesis, it was predicted that levels of species diversity would be elevated at the point of intermediate disturbance along this anthropogenic disturbance gradient where forested and open areas co-occur in significant proportions. Secondly, it was envisioned that this peak in diversity would reflect the accumulation of niches - a consequence of partial replacement of semi-natural and managed forest by open and agricultural habitats. Such a mosaic was predicted to support significant elements of forest-adapted communities in an essentially agricultural landscape (Petit & Usher 1998; de la Pena *et al.* 2003).

It is not possible through either a lack of specialist knowledge or logistical constraints, to survey all the biological diversity in a given area (Kremen 1994; Oliver & Beattie 1996). Consequently surrogates of total biodiversity are commonly used to make a rapid assessment of the relative contribution of different types of land-use or habitat to an area's biodiversity (Kremen 1992, 1994; Oliver & Beattie 1996; Prendergast 1997; Duelli & Obrist 1998; Stork 1999). This study uses carabid beetle assemblages as a surrogate of biodiversity to assess the response of invertebrate communities to the twin anthropogenic impact of fragmentation and land-use intensification. Carabidae were surveyed along a gradient of land-use in Northern Scotland, corresponding to a decline in the proportion of forest cover and concomitant increase in the amount of agricultural land. Carabid beetles were chosen as study organisms because they are widely-distributed and abundant (Thiele 1977), sensitive to landscape structural heterogeneity and land-use (Dennis *et al.* 1997; Davies & Margules 1998; Ribera *et al.* 2001; Dennis *et al.* 2002; Brose 2003), are both taxonomically and ecologically diverse (Ribera *et al.* 2001; Cole *et al.* 2002), and yet well-known having been studied intensively (Thiele 1977). Furthermore, recent studies have shown that despite species turnover between habitats or regions, the response of carabid communities to disturbance is consistent (Ribera *et al.* 2001; Niemela *et al.* 2002).

By quantifying carabid diversity under different land-use scenarios this study aims to improve the understanding of the interrelationship between this beetle community and landscape structural heterogeneity, and thus contribute to the development of standardised systems for the monitoring of the interaction between biodiversity and land-use. Two specific predictions are tested: (i) carabid diversity (species richness and abundance) will be highest at the point along the gradient with the greatest landscape heterogeneity- a consequence of intermediate levels of disturbance (IDH) (Connell 1978). This pattern will be evaluated further by an assessment of compositional patterns and species autecology; and (ii) carabid community structure will reliably signal landscape structural heterogeneity and will be correlated with site-specific features.

3.2 Methods

3.2.1 Land-use units and carabid sampling

Six land-use units (LUU) representing a land-use gradient, numbered from LUU1 (lowest intensity land-use) to LUU6 (highest intensity land-use), were set up in the area to the west of CEH Banchory (57°01'- 07' N, 02°61'- 87' W) (Table 3-1). Each LUU was represented by a 1 km by 1 km square (Figure 3-1a) and these LUUs were all a maximum of 10 km from each other. The LUUs were visually selected according to an ideal, pre-defined set of criteria corresponding to the type of land-uses predominating within this spatial unit (LUU1 & 2 100 % forest; LUU3: 70 % forest; LUU4: 50 % - forest, 50 % - open habitat; LUU5: 70% managed grassland; LUU6: 70 % arable) (Table 3-1, Figure3-1b). We sampled each LUU on a systematic 4 x 4 grid giving 16 sampling points (Table 3-2) each separated by 200m from neighbouring points and the edge of the square (Figure3-1a). All biotic and abiotic data were gathered on this grid. The choice of a systematic grid rather than a stratified design to sample the beetle communities in different habitats resulted from the broader research framework in which this study fits: birds were also sampled in the LUUs and are distributed at coarser spatial scales than beetles, hence the systematic grid is a compromise between the ideal sampling strategy for different taxa (Anon 2003).

Carabid beetle communities were sampled using pitfall trapping: four traps (with plastic rain shields to prevent flooding) were placed 4m apart in a regular 2 x 2 grid at each sampling point. Traps consisted of polypropylene cups, 8.5 cm diameter and 10 cm deep, partially filled with 80% ethylene glycol to act as a preservative and killing agent, and a small amount of unscented detergent. Traps were emptied at 2-week intervals between 4 May and 30 August 2001 (15 weeks continuous trapping effort), and 8 April and 26 August 2002 (20 weeks trapping effort). The length of the trapping period was set to provide as complete a sample of the communities as logistically possible. The later start in 2001 was a consequence of the foot and mouth epidemic resulting in a delay in access to the study sites. On each occasion the contents of the four traps at each sampling point were pooled to give one sample per point in the sampling grid. The catch was sorted and identified to species using Lindroth (1974), nomenclature followed Luff and Duff (2004).

Figure 3-1. Figure 3-1a. Location, dimension and sampling grid of the six land–use units (LUUs) in Aberdeenshire, Scotland, UK. Each LUU was a 1km^2 quadrat with a nested grid of sampling points distributed at 200m intervals from each other and the edge of the square. No LUU was more than a distance of 10km from the others. All biological and environmental data were gathered on the intersections of this grid. Figure 3-1b. Habitat composition and context of the six LUUs showing the landscape heterogeneity of the LUUs and surrounding areas. These images were produced with ARCGIS using a fused satellite image (LandsatTM & IRS) of the study area.

Figure 3-1a

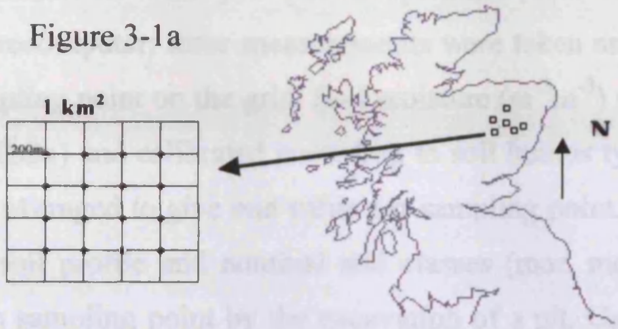
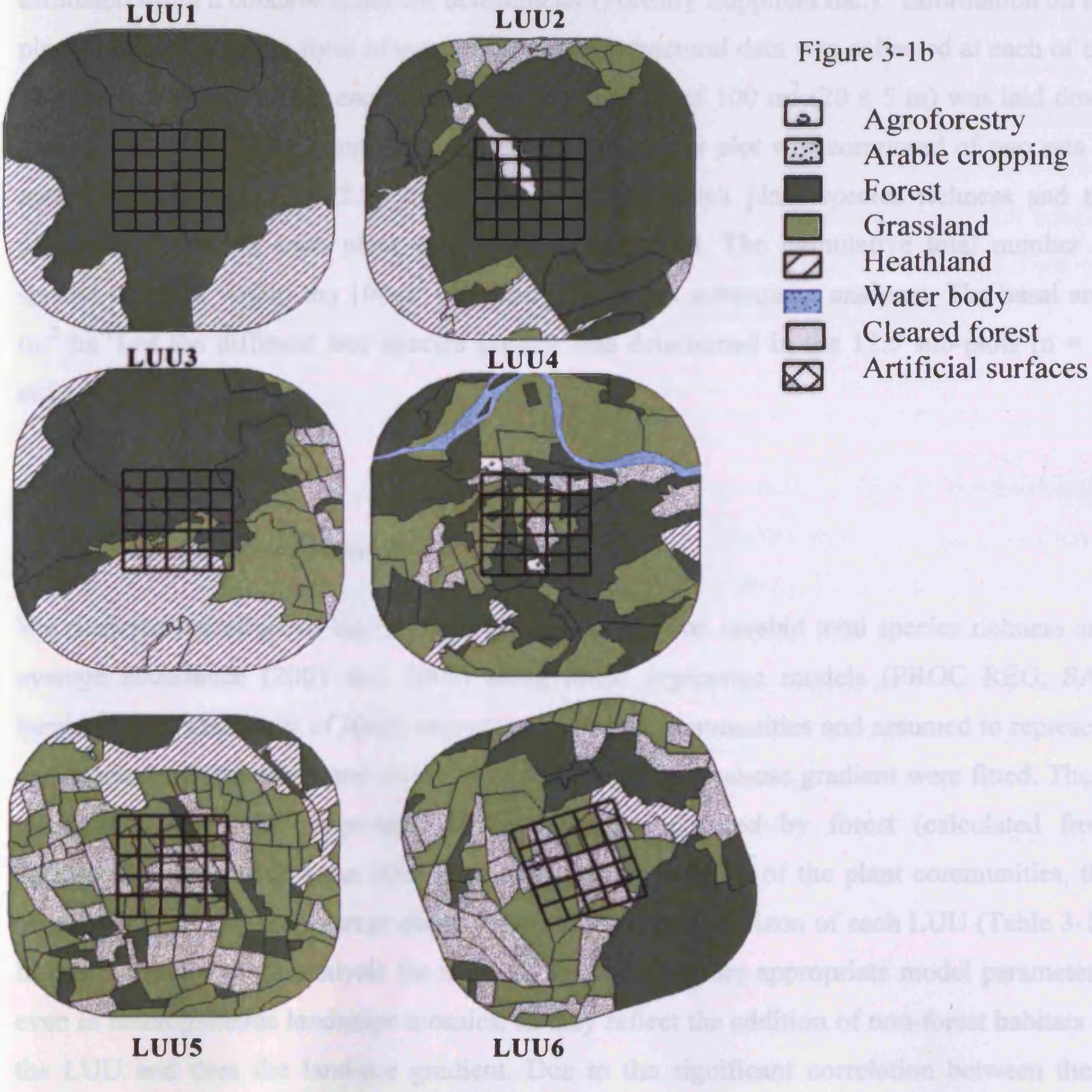


Figure 3-1b



3.2.2 Environmental variables

At each sampling point along the gradient potential explanatory variables were collected to characterise the site and to attempt to identify those factors structuring the beetle communities. Soil pH and temperature data were collected using a Hanna HI 9024 microcomputer; three measurements were taken and averaged to give a single value for each sampling point on the grid. Soil moisture ($m^{-3}m^{-3}$) was determined using a theta probe (Delta-T ML2x) and calibrated according to soil humus type. Again three measurements were taken and averaged to give one value per sampling point. The depth (cm) of the organic horizon in the soil profile and nominal soil classes (mor, moder or mull humus) were determined for each sampling point by the excavation of a pit. Canopy density over the sampling point was estimated using a concave spherical densiometer (Forestry Suppliers Inc.). Information on the plant community in the form of compositional and structural data was collected at each of the 16 sampling points within each site. A rectangular plot of 100 m^2 (20 x 5 m) was laid down around the centre of the sampling point. This rectangular plot was composed of two sets of nested sub-plots of 1, 5,12.5, 25 and 50m^2 within which plant species richness and the percentage cover of each plant species was determined. The cumulative total number of species sampled within the 100m^2 was then used in the subsequent analyses. The basal area (m^2 ha^{-1}) of the different tree species present was determined in the 12.5 sub-plots ($n = 2$) only.

3.2.3 Statistical analysis

3.2.3.1 Patterns in carabid diversity

We analysed the effect of the land-use gradient ($n = 6$) on carabid total species richness and average abundance (2001 and 2002) using linear regression models (PROC REG, SAS version 8.1). Parameters of likely importance to beetle communities and assumed to represent the structure, productivity and intensity of soil use of the land-use gradient were fitted. These parameters were: the proportion of the landscape covered by forest (calculated from Landsat/IRS data sets)(Anon 2003), the total species richness of the plant communities, the average soil pH and the average depth (mm) of the organic horizon of each LUU (Table 3-1). In this landscape-scale analysis the mean of soil variables are appropriate model parameters, even in heterogeneous landscape mosaics, as they reflect the addition of non-forest habitats to the LUU and thus the land-use gradient. Due to the significant correlation between these environmental parameters only their marginal effects on carabid species richness and abundance are reported here.

The composition of the beetle community at the sampling point level was also evaluated to gain insight into the observed patterns of carabid abundance and species richness between agricultural sampling points along the gradient. This was done using information on the ecology and known distribution of individual species (e.g. body size, open - habitat specialist, collembolan predator etc) drawn from Lindroth (1974, 1985, 1986), Hyman and Parsons (1992) and Anon (2002b). This evaluation of compositional differences between sampling points is a qualitative analysis - no formal statistical analysis could be used due to restricted sample size and with the sampling points being nested within LUU (risk of pseudoreplication, Hurlbert 1984). Bearing this caveat in mind a number of questions were posed using data from sampling points in agricultural grassland (n = 26, Table 3-2) from the predicted high (LUU4) and low (LUU5 and 6) points of the 'intensification' end of the land-use gradient: (i) Do these samples show equivalent levels of mean carabid species richness and abundance? (ii) Do individual species recorded from grassland-dominated sampling points in LUU4 (n = 9) and LUU6 (n = 5) show differences in their relative average abundance? (iii) Are species commonly recorded from open and agricultural habitats present in the mosaic land-use (LUU4) that are absent in the more intensively farmed landscapes (LUU5 and 6)?

3.2.3.2 Carabid community structure

Dominance structure of the carabid beetle communities from each LUU was assessed using species rank-abundance plots. The species-specific abundance data were summed over time to give a single value for each species at each sampling point along the gradient in each year. Factors responsible for the structuring of the carabid beetle communities were identified using ordination analysis (CANOCO ver. 4.5). To ensure that the ordination was not unduly influenced by individual species the rarest 1% of species were excluded, then $\log_e$ (x+1) transformed to minimise the impact of the most abundant species on the analysis, and the least common species were down-weighted using the options available in CANOCO (Jongman *et al.* 1995, ter Braak and Šmilauer 1998).

Table 3-1. Location, description and composition of the land-use unit gradient along which carabid beetles were collected. Coordinates are decimal degrees of the first sampling point in each LUU e.g. LUU1.1, LUU2.1 etc. The soil parameters are derived from three measurements taken at each sampling point in each LUU and then averaged for the LUU. Plant *S* is the total plant species richness recorded for each LUU.

LUU	Landscape description	Plant community	Arable	Grassland	Forest	Plant *S*	Soil		Latitude-Longitude
		(dominant)	(%)	(%)	(%)	(n)	pH	O-horizon (cm)	
1	Old-growth forest	Caledonian pinewood	0	0	100	9	3.9	28.9	57.019057 03.140373
2	Managed forest	Scots pine plantation	0	0	88.5	10	3.9	9.0	57.047952 03.247554
3	Forest-dominated mosaic	Scots pine-birch forest	0	16.7	65	20	4.3	10.7	57.015483 03.309506
4	Mixed-use mosaic	Grazed grassland	17.3	30.9	49.8	29	5.5	1.7	57.068030 03.127909
5	Pasture dominated	Mown grassland	35	57.6	7.4	15	6.2	0.1	57.030556 03.375779
6	Arable dominated	Arable cropping	51.7	43	1.6	11	6.2	0.1	57.143960 03.189496

Table 3-2. Distribution of the sampling points among the major habitat classes in the LUUs sampled. LUU4 only has 15 sampling points because one point fell in an arable field and access to this point was denied.

LUU	Forest					Pasture		Arable
	Coniferous			Deciduous	Mixed	Permanent	Rotational	Rotational
	Natural	Managed						
		Exotic	Native					
1	16	0	0	0	0	0	0	0
2	0	1	15	0	0	0	0	0
3	0	0	7	3	2	4	0	0
4	0	1	5	0	0	3	6	0
5	0	1	0	0	0	0	12	3
6	0	0	0	1	0	1	4	10

Species abundance data were first analysed using detrended correspondence analysis (DCA) with detrending by segments to identify whether, theoretically, an environmental gradient existed in the species abundance data set and to identify whether the beetle community demonstrated a strongly unimodal or linear response to that gradient. Subsequently the data were analysed with a canonical correspondence analysis (CCA) relating the species abundance data to measured environmental variables. Scaling was focused on inter-species distances with bi-plot scaling being applied. The significance of these environmental factors in structuring the carabid communities was determined with a forward selection procedure using Monte-Carlo tests (999 permutations). Environmental variables not of primary interest within the objectives of this study (e.g. altitude of sampling point) were subsequently fitted as covariates, thus the final model is a partial CCA controlling for these effects and constraining the Monte-Carlo permutations to operate within blocks defined by the LUU. Inflation factors in the CCA model were inspected to check for colinearity between significant environmental variables.

3.3 Results

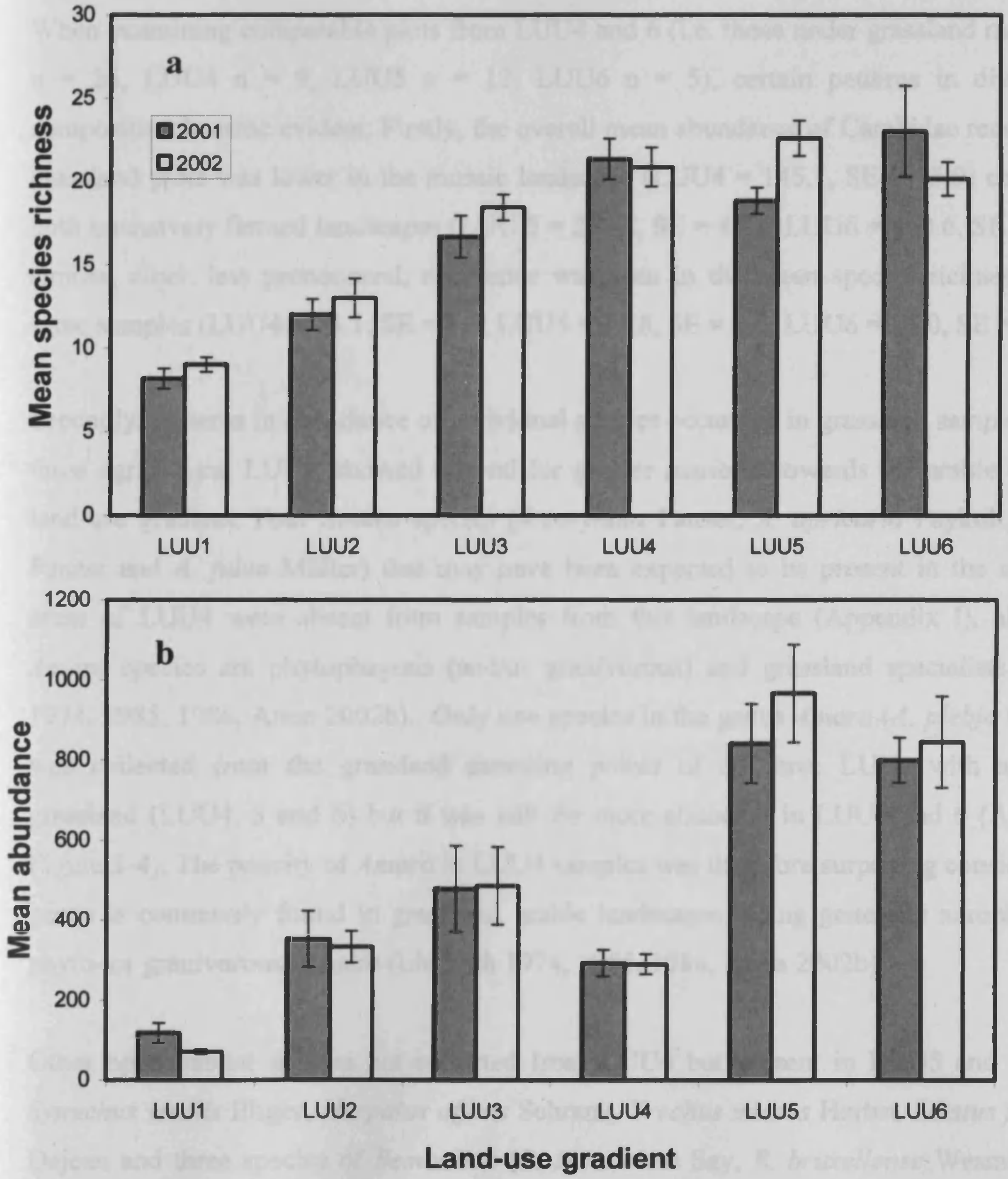
3.3.1 Patterns in carabid diversity

A total of 17,494 individuals from 51 species were collected in 2001, and 20,935 individuals from 54 species in 2002. The five most numerous species in 2001 were *Nebria brevicollis* Fabricius (3,059, 17% of total), *Pterostichus madidus* Fabricius (2,993, 17 %), *Bembidion tetracolum* Say (1,334, 8%), *Anchomenus dorsalis* Pontopiddan (1,164, 7%) and *Calathus micropterus* Duftscmid (1,030, 6%), representing 55% of the total fauna collected. The most numerous species in 2002 were *N. brevicollis* (5,531, 26%), *P. madidus* (3,192, 15%), *Agonum muellerii* Herbst (1,537, 7%), *B. tetracolum* (1,168, 6%) and *Pterostichus niger* Schaller (964, 5%), representing 59 % of the total collected (Appendix I).

In both years of study an increase in species richness was recorded as the proportion of forest declined, and open, agricultural habitat increased along the gradient from LUU1 to LUU6. In 2001, the highest species richness was found at LUU6, the arable site, while in 2002 the greatest number of species was collected from LUU5, the grassland dominated site (Figure 3-2a). The lowest value of species richness in both years was recorded at LUU1, the semi-natural forest site (Figure 3-2a). The average abundance of Carabidae was greatest in the most disturbed and open landscapes of LUU5 and LUU6 in both years of the study (Figure 3-2b).

When the species abundance data were ranked, differences in the dominance structure of the carabid communities between LUUs were observed (Figure 3-3). The forest landscapes (LUU1 and 2) had carabid communities dominated by a few abundant species and supported more rare species (relative to overall species richness) than the other landscapes. The mosaic and agricultural landscapes (LUU3–6) supported more even assemblages with more species of equivalent abundance. In general, the less forested the landscape the more species and greater abundance it could support.

Figure 3-2. Figure 3-2a.Mean species richness (± SE) of Carabidae; Figure 3-2b. Mean abundance (± SE) of Carabidae per land-use unit (LUU)



At the LUU scale (1 km^2 x 6) the proportion of forest in the landscape was a good, inverse predictor of both the average carabid abundance ($F_{1,4} = 22.32$, $P = 0.009$, Adj. $r^2 = 0.81$) and total species richness ($F_{1,4} = 16.89$, $P = 0.014$, Adj. $r^2 = 0.76$). Soil pH also showed a notable, but marginally non-significant, inverse relationship with carabid abundance ($F_{1,4} = 7.31$, $P = 0.053$, Adj. $r^2 = 0.56$) and a highly significant relationship with species richness ($F_{1,4} = 16.06$, $P = 0.016$, Adj. $r^2 = 0.75$). The depth of the organic horizon in the soil profile predicted species richness well ($F_{1,4} = 8.92$, $P = 0.040$, Adj. $r^2 = 0.61$) but not abundance ($F_{1,4} = 5.14$ $P = 0.085$, Adj. $r^2 = 0.45$). Plant community species richness predicted neither carabid abundance ($F_{1,4} = 0.03$ $P = 0.866$, Adj. $r^2 = -0.24$) nor carabid species richness ($F_{1,4} = 1.69$ $P = 0.263$, Adj. $r^2 = 0.12$).

When examining comparable plots from LUU4 and 6 (i.e. those under grassland management n = 26, LUU4 n = 9, LUU5 n = 12, LUU6 n = 5), certain patterns in diversity and composition became evident. Firstly, the overall mean abundance of Carabidae recorded from grassland plots was lower in the mosaic landscape (LUU4 = 145.1, SE = 35.9) compared to both intensively farmed landscapes (LUU 5 = 253.8, SE = 41.1; LUU6 = 460.6, SE = 94.6). A similar, albeit less pronounced, difference was seen in the mean species richness of these same samples (LUU4 = 13.1, SE = 1.0; LUU5 = 15.8, SE = 0.6; LUU6 = 16.0, SE = 1.9).

Secondly, patterns in abundance of individual species occurring in grassland samples from all three agricultural LUUs, showed a trend for greater numbers towards the arable end of the land-use gradient. Four *Amara* species (*A.eurynota* Panzer, *A. apricaria* Paykull, *A. aulica* Panzer and *A. fulva* Müller) that may have been expected to be present in the agricultural areas of LUU4 were absent from samples from this landscape (Appendix I), all of these *Amara* species are phytophagous (and/or granivorous) and grassland specialists (Lindroth 1974, 1985, 1986, Anon 2002b). Only one species in the genus *Amara* (*A. plebja* Gyllenhal) was collected from the grassland sampling points of all three LUUs with agricultural grassland (LUU4, 5 and 6) but it was still far more abundant in LUU5 and 6 (Appendix I, Figure 3-4). The paucity of *Amara* in LUU4 samples was therefore surprising considering this genus is commonly found in grass and arable landscapes, being generally xerophilous and phyto- or granivorous in habit (Lindroth 1974, 1985, 1986, Anon 2002b).

Other open habitat species not collected from LUU4 but present in LUU5 and 6 include: *Synuchus vivalis* Illiger, *Harpalus affinis* Schrank, *Trechus micros* Herbst, *Leistus fulvibarbis* Dejean and three species of *Bembidion* (*B. tetracolum* Say, *B. bruxellense* Wesmael and *B.*

guttula Fabricius) (Appendix I). The majority of species that were collected from grassland areas of both LUU4 and LUU6 were relatively more abundant in the situation where a greater proportion of the landscape was under intensive rotational management (LUU6) (Figure 3-4). *Anchomenus dorsalis, Calathus melanocephalus* L. *sensu strictu, Clivina fossor* L. and *Pterostichus melanarius* Illiger, all common species in open grassland habitats (Lindroth 1974, 1985, 1986, Anon 2002b) were far more abundant in LUU6 (Figure 3-4). *Nebria brevicollis*, a species commonly considered to be eurytopic (Lindroth 1974, 1985, 1986, Anon 2002b), showed the strongest preference toward the arable end of the gradient (Figure 3-4).

Figure 3-3. Species rank-abundance plot for the six LUUs from 2001 (illustrative example)

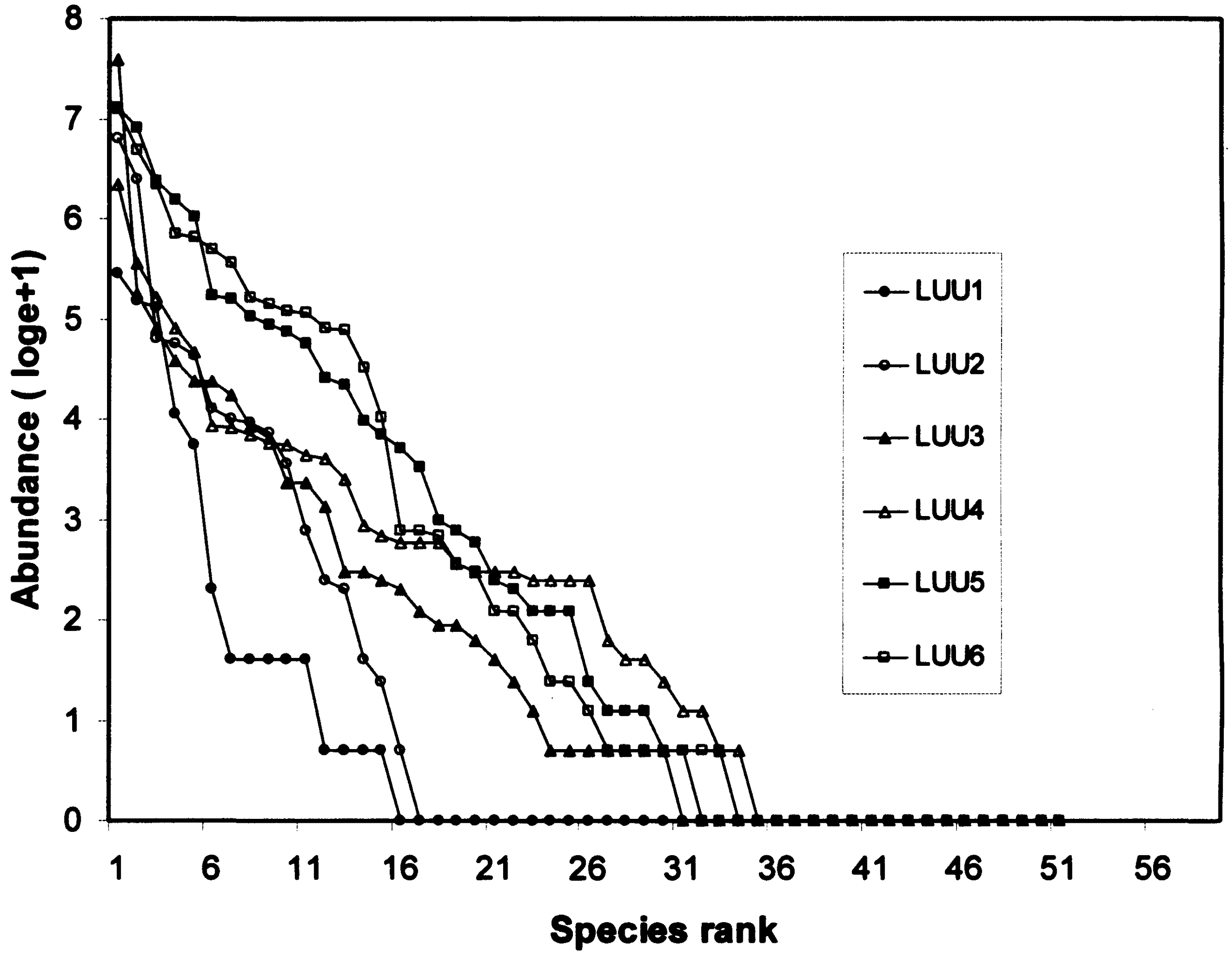
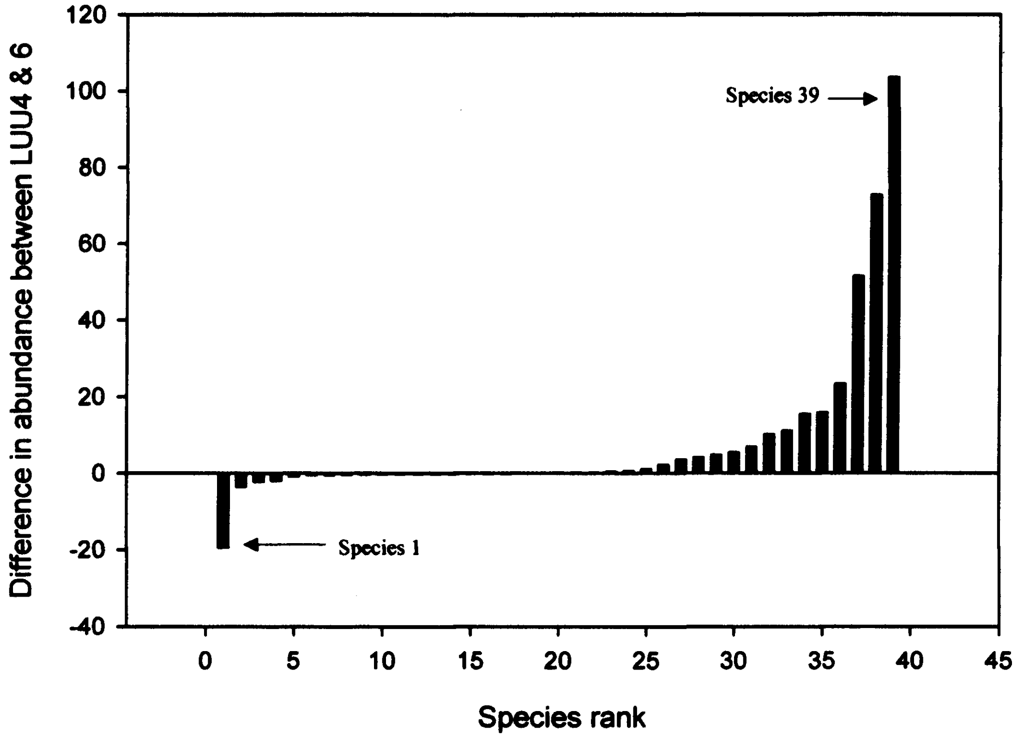


Figure 3-4. Relative difference in abundance between the Carabidae recorded from grassland sampling points in LUU4 (n = 9) and LUU6 (n = 5). Ranked differential abundance of all species recorded in one or both of the LUUs. Negative values indicate a species was recorded in greater abundance in the mosaic landscape (LUU4) while positive values indicate a trend in abundance towards the arable-dominated landscape (LUU6). See Appendix I for full details of species names.

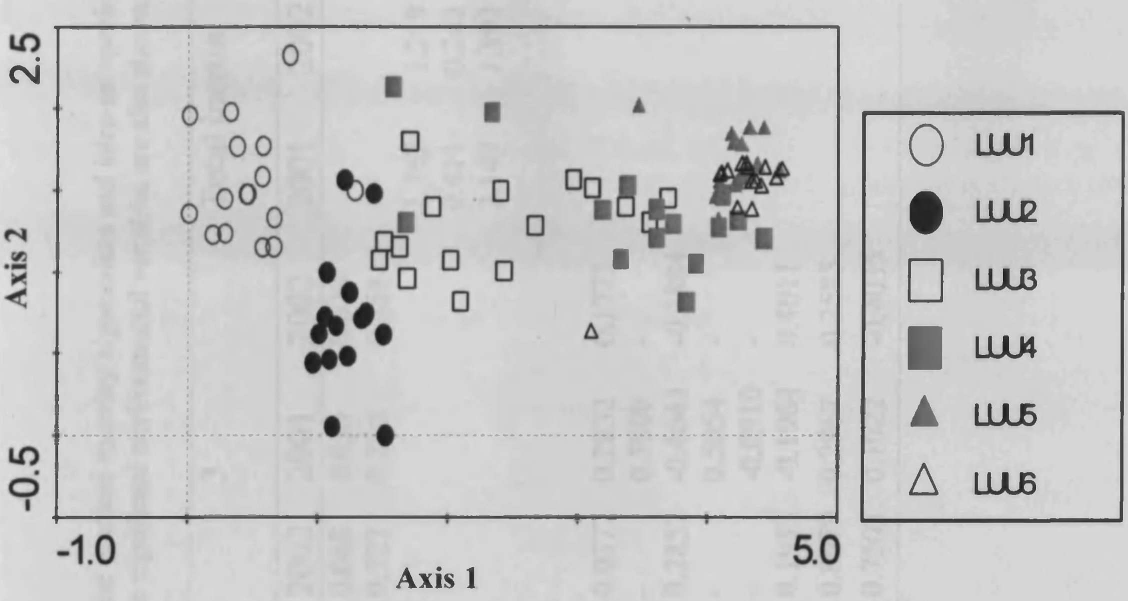


Rank	*Species*	*Value*
1.	*C. fuscipes*	-19.43
2.	*P. nigrita agg.*	-3.63
3.	*P. atrorufus*	-2.28
4.	*P. strenuus*	-2.03
5.	*A. aenea*	-0.88
6.	*A. familaris*	-0.50
7.	*C. violaceus*	-0.50
8.	*L. terminatus*	-0.36
9.	*C. rotundicollis*	-0.35
10.	*P. assimilis*	-0.25
11.	*A. lunicollis*	-0.25
12.	*C. problematicus*	-0.25
13.	*N. rufescens.*	-0.25
14.	*P. adstrictus*	-0.25
15.	*A. bifrons*	-0.13
16.	*C. nemoralis*	-0.13
17.	*C. caraboides*	-0.13
18.	*A. fulva*	0.00
19.	*H. affinis*	0.00
20.	*L. fulvibarbis*	0.20
21.	*P. oblongopunctat*	0.20
22.	*B. mannerheimi*	0.23
23.	*T. micros*	0.40
24.	*S. vivalis*	0.60
25.	*B. lampros*	1.08
26.	*N. bigutatus*	2.30
27.	*P. niger*	3.68
28.	*T. quadriastriatus*	4.15
29.	*B. guttula*	4.80
30.	*L. pilicornis*	5.48
31.	*A. plebja*	6.93
32.	*A. muelleri*	10.15
33.	*C. fossor*	11.13
34.	*C. melanocephalu*	15.45
35.	*P. madidus*	15.80
36.	*B. tetracolum*	23.40
37.	*A. dorsalis*	51.53
38.	*P. melanarius*	72.73
39.	*N. brevicollis*	103.60

3.3.2 Carabid community structure

Detrended Correspondence Analysis (DCA) revealed that the carabid communities were showing a strongly unimodal relationship to the environmental gradient (axis 1: 2001 eigenvalue = 0.76, gradient length = 4.57 SD; 2002 eigenvalue = 0.68, gradient length = 4.14 SD). The LUUs can be discriminated by their faunal composition: the forested sites (LUU1 and 2) are clearly separated from the open habitats (LUU5 and 6) in the ordination plot, and the more heterogeneous mosaic landscapes (LUU3 and 4) intermediate between the two extremes of the gradient (Figure 3-5). In addition, the ordination plot clearly shows that the carabid communities in LUU1 and LUU2 are quite distinct from each other despite these environments being dominated by the similar plant communities (Figure 3-5, Table 3-1).

Figure 3-5. Detrended correspondence analysis (DCA) of Carabidae along a land-use gradient from 2001 (illustrative example). Axis 1 eigenvalue = 0.761 Axis 2 eigenvalue = 0.12. Length of gradient along first axes = 4.572.



CCA analysis showed that the structure of the carabid community was significantly correlated with environmental variables in both years (2001 sum of canonical eigenvalues of first axis = 0.171, Monte Carlo global permutation test P = 0.001; 2002 sum of canonical eigenvalues of first axis = 0.127, Monte Carlo global permutation test P = 0.005). LUU was a significant influence on the species data in the full, unconstrained model accounting for 7.5% (eigenvalue = 0.10, P = 0.001) and 6.4% (eigenvalue = 0.07, P = 0.001) of the inertia in 2001 and 2002, respectively. Sampling point altitude accounted for a significant amount of the variation in carabid community structure within each LUU explaining 8.3 % (eigenvalue = 0.11, P = 0.001) and 8.2% (eigenvalue = 0.09, P= 0.001) of the inertia in 2001 and 2002, respectively. These two significant environmental variables were subsequently fitted as covariates to account for this variation, and the model was rerun as a partial CCA constrained by LUU. Overall, the partial CCA model accounted for 30.0 % and 19.8% of the variation in the species data in 2001 in 2002, respectively (Table 3-3, Figure 3-6). The land-use gradient (LUU1-6), fitted as a categorical covariable in this partial model, explained a further 36.6 % and 34.8 % of the total inertia in the species data in 2001 and 2002, respectively (Table 3-3).

Table 3-3. Partial canonical correspondence analysis (pCCA) of Carabidae along the land-use gradient showing eigenvalues and intra-set species environment correlation coefficients for the first three environmental axes. Correlation coefficients for the significant environmental variables are also shown.

Axes	1		2		3		Total inertia	
Year	2001	2002	2001	2002	2001	2002	2001	2002
Eigenvalue	0.169	0.108	0.083	0.068	0.056	0.026		
Species-environment correlation	0.863	0.779	0.786	0.727	0.738	0.558		
Sum of all unconstrained eigenvalues							1.362	1.219
Sum of all canonical eigenvalues							0.411	0.242
Total inertia							2.149	1.893
Intra-set correlation coefficients								
Canopy density	-0.8748	-0.9497	0.0365	0.0372	0.2832	0.1772		
Moder soil	-0.1289	-	0.2005	-	0.5806	-		
Mull soil	0.6905	0.7270	0.2974	0.2852	-0.4643	-0.3884		
Depth of organic horizon	0.2532	-	-0.3371	-	0.5054	-		
Soil pH	0.6136	-	-0.0527	-	-0.0910	-		
Soil moisture	0.0762	0.2664	0.3202	0.1953	-0.1964	0.4011		
Plant species richness	0.1700	0.1614	0.8355	0.8979	0.2967	0.2585		
Birch spp. cover	-0.1810	-0.3055	0.7400	0.7503	0.1022	-0.4035		

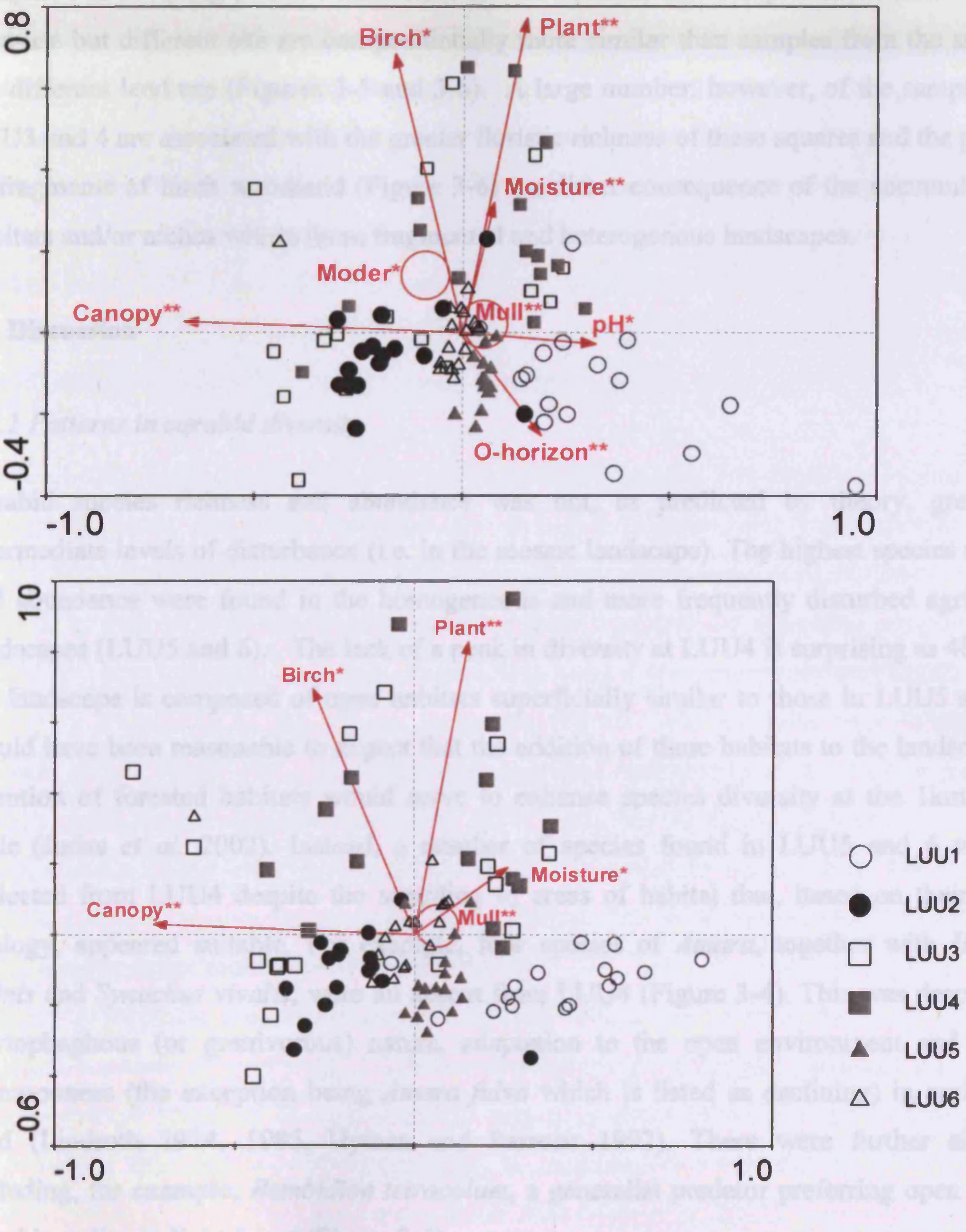
After controlling for the overall effect of the land-use gradient it was possible to identify a number of environmental parameters that differentiate the carabid communities along the gradient. In 2001, there were eight environmental variables that significantly explained the inertia in the species abundance data, whereas in 2002 there were only five, the latter being significant in both years (Table 3-4).

Table 3-4. Significant environmental parameters fitted step-wise by forward selection in a partial CCA model. Eigenvalues, and F and P values from Monte-Carlo global permutation tests (999 permutations constrained by LUU as a blocking factor).

Environmental parameter	**Eigenvalue**		**F-values**		**P**	
	2001	2002	2001	2002	2001	2002
Canopy density	0.14	0.10	10.09	7.97	0.001	0.001
Moder soil	0.03	-	2.38	-	0.01	-
Mull soil	0.03	0.02	2.69	2.20	0.006	0.009
Depth of organic horizon	0.05	-	3.83	-	0.002	-
Soil pH	0.03	-	2.22	-	0.01	-
Soil moisture	0.02	0.02	2.07	1.64	0.003	0.026
Plant species richness	0.07	0.06	5.43	5.12	0.001	0.001
Birch spp. cover	0.05	0.04	3.79	3.26	0.01	0.01

The high acidity of the soil, possibly a consequence of the accumulation of a deep litter and organic layer in the soil profile and granitic bedrock, was structuring the carabid community in LUU1 (Figure 3-6a). Furthermore, the strong, negative relationship of the beetle community in LUU1 to canopy density reflects the open, structure of Caledonian pinewood and the nature of the adapted fauna (Figure 3-6). This contrasts to the situation in LUU2 where, despite sharing a similar plant community in compositional terms, the structural differences and implicitly more frequently disturbed environment lead to a different carabid assemblage being found in this landscape - a fauna indicative of dense, closed canopy forest (Figure 3-6).

Figure 3-6. Partial canonical correspondence analysis (pCCA) sample-environment biplot of the Carabidae a) 2001 and b) 2002. Continuous environmental variables are represented by solid line vectors, nominal environmental variables by large, open circles. Environmental variable abbreviations: Plant = plant species richness, Birch = basal area (m^2) of *Betula* spp., Canopy = canopy density, pH= soil pH, Moisture = soil moisture, O-horizon = depth (mm) of the organic horizon, Mull or Moder = soil humus class. Significance of environmental variables determined by Monte-Carlo global permutation tests (constrained by LUU) * <0.05, **<0.01



Both agriculturally dominated sites (LUU5 and 6) possess a fauna that is associated with mull soils and, while still separated from each other in the tri-plot, cluster closer together than the other LUUs in the ordination. This shows a clear separation between the forested and open agriculturally dominated sites (Figures 3-5 and 3-6). The mosaic sites (LUU3 and 4) show a wider scatter in the ordination plot reflecting the overall heterogeneity of the landscape in those squares. There is a greater degree of sample similarity with points in other LUUs compared to sampling points within these mosaic squares, thus samples taken from the same land-use but different site are compositionally more similar than samples from the same site but different land-use (Figures 3-5 and 3-6). A large number, however, of the samples from LUU3 and 4 are associated with the greater floristic richness of these squares and the presence of fragments of birch woodland (Figure 3-6) - a direct consequence of the accumulation of habitats and/or niches within these fragmented and heterogenous landscapes.

3.4 Discussion

3.4.1 Patterns in carabid diversity

Carabid species richness and abundance was not, as predicted by theory, greatest at intermediate levels of disturbance (i.e. in the mosaic landscape). The highest species richness and abundance were found in the homogeneous and more frequently disturbed agricultural landscapes (LUU5 and 6). The lack of a peak in diversity at LUU4 is surprising as 48.2 % of the landscape is composed of open habitats superficially similar to those in LUU5 and 6. It would have been reasonable to expect that the addition of these habitats to the landscape and retention of forested habitats would serve to enhance species diversity at the 1km^2 spatial scale (Judas *et al.* 2002). Instead, a number of species found in LUU5 and 6 were not collected from LUU4 despite the sampling of areas of habitat that, based on their known ecology, appeared suitable. For example, four species of *Amara*, together with *Harpalus affinis* and *Synuchus vivalis*, were all absent from LUU4 (Figure 3-4). This was despite their phytophaghous (or granivorous) nature, adaptation to the open environment and general commonness (the exception being *Amara fulva* which is listed as declining) in agricultural land (Lindroth 1974, 1985, Hyman and Parsons 1992). There were further absentees including, for example, *Bembidion tetracolum*, a generalist predator preferring open country yet able to live in light forest (Figure 3-4).

These absentee species were collected from the arable fields (barley) or intensively managed grassland (silage and grazing) in LUU5 and 6. No sampling point in LUU4 was located either in or adjacent to arable fields, firstly because access was denied to the one arable sampling point in LUU4, and secondly, reflecting the relatively low proportion of arable habitat in that landscape (Figure 3-1, Tables 3-1 and 3-2). In addition, 86% of samples from LUU5 and 6 containing these missing species were obtained from sampling points at or within 10m of edge features such as dry-stone walls, field margins, hedgerows and drainage ditches, or combinations thereof. These features are important to carabid beetles and other invertebrates (Petit & Usher 1998; Holland & Fahrig 2000; Meek *et al.* 2002; de la Pena *et al.* 2003) with implications for biocontrol – these landscape features are likely to be important as over-wintering sites and refuges enabling predator (and herbivore) populations in agricultural landscapes to persist and re-colonise fields after periodic disturbances (Ostman *et al.* 2001; Weibull *et al.* 2003). These features are, however, also present in the mosaic LUU4 (77 % of grassland sampling points were within 10m of edge features) so are not entirely convincing hypotheses for the absence of these species from that location.

Open-habitat species that did occur in LUU4 were, in general, less abundant in that location than in the more intensively managed site at LUU6 (Figure 3-4). Some species (*Nebria brevicollis, Anchomenus dorsalis* and *Pterostichus melanarius*) demonstrated a strong gradient in their relative abundance, occurring more frequently in grassland sampling points within the more intensive landscape (Figure 3-4). Only a few species showed trends towards increasing abundance in the mosaic landscape (Figure 3-4), of these two - *Pterostichus strenuus* and *P. nigrita agg.* - are commonly associated with woodland and may be considered tourists from nearby forest stands. The third, *Calathus fuscipes*, showing the strongest preference for LUU4 over LUU6 (Figure 3-4), is adapted to open habitat but with quite specific edaphic requirements (sandy / clay substrate rich in organic matter (Lindroth 1974, 1985, 1986)), better met by LUU4 (A.J.Vanbergen *pers. obs.*). Overall, most species showed a slight to moderate directional gradient in their abundance towards the more intensively managed situation (Figure 3-4). A number of specialised collembola predators e.g. *Trechus quadriastriatus* appeared to favour LUU6 and it is conceivable that the variation in the abundance of these species may in some part be explained by a tendency of collembola to be more abundant in heavily fertilised agricultural soils (Cole *et al.* 2002).

These patterns of occurrence lead to hypotheses requiring further testing and caveats regarding these data: (i) Species absences may merely reflect the existence of a local fauna at

LUU4 (Kinnunen *et al.* 2001), difficult to refute in the absence of a replicate mosaic site; (ii) The spatial structure of the mosaic of land-use may be impacting negatively on certain species or the whole community of open habitat species (Judas *et al.* 2002) either through a high level of insularity between comparable habitat types (Kinnunen & Tiainen 1999) or a lower number of beneficial habitats in the mosaic e.g. arable fields (Petit & Usher 1998; de la Pena *et al.* 2003); (iii) Small scale heterogeneity (at the sampling plot level) may be responsible for the observed patterns. It is obvious that at the 1km^2 scale the landscapes LUU5 and 6 are more homogenous than LUU4 (i.e. less patches of woodland; Figure 3-1, Table 3-2), but it may be that the more frequent disturbance arising from rotational crop management at LUU5 and LUU6 can produce spatio–temporal heterogeneity (e.g. in resource availability or edge effects arising from the juxtaposition of field margins and crop habitats) at fine scales (e.g. individual fields). Such fine-scale heterogeneity could have the effect of increasing beetle species richness and abundance, and it is possible that it is at this fine scale and not at the landscape scale that carabid beetles are most sensitive to disturbance (Niemela *et al.* 1996; Dennis *et al.* 1997; Dennis *et al.* 2002; Koivula *et al.* 2002; Brose 2003); and (iv) The lack of certain open-habitat species from LUU4 may be an artefact of the sampling design: the regular grid may, by chance, have failed to sample key carabid habitats (e.g. agricultural fields and field margins), so accounting for their absence from the samples but not, in reality, from the landscape.

3.4.2 Carabid community structure

DCA analysis showed that there were considerable differences between carabid assemblages along the land-use gradient. The LUU was a significant determinant of carabid community structure accounting for over a third of the inertia in the beetle community data when fitted as a covariable in the CCA. In the absence of a replicate gradient, this pattern should be interpreted with caution, but by accounting for this variation landscape attributes or features that are significant in structuring these beetle assemblages could be identified. Global permutation tests identified that the density of tree canopy, a mull soil profile and the plant species richness (Table 3-4) were the most important factors that affect these carabid assemblages. Soil pH and the coverage of birch (*Betula* spp) were also significant features of these landscapes (Table 3-4). The Caledonian pinewood fauna at LUU1 was primarily associated with low pH and a deep organic horizon in the soil profile together with low levels of canopy closure, indicating that these carabid communities require an undisturbed environment, probably with certain habitat features (e.g. deadwood). Indeed, this habitat supports few abundant species and many more uncommon species compared with the other environments in this study (Figure 3-3). *Cicindela campestris*, for example, while not threatened, is very locally distributed in the landscape gradient studied here. Furthermore, this pinewood habitat supported the greatest abundance of *Pterostichus oblongopunctatus*, a notable species of restricted distribution in the UK (recorded from < 100, 10 km^2 in Britain) (Hyman & Parsons 1992). This species occurred at much lower numbers in the forested areas of the other landscapes, and there was a notable drop in the abundance of this species between LUU2 and 3, where the forest is more fragmented (Appendix I).

The carabid fauna of the Scots pine plantation (LUU2) was clearly separated in the ordination space from that of Caledonian pinewood (LUU1) (Figures 3-5 and 3-6) - an unexpected result given the vastly greater area of land under plantation and highlighting further the conservation value of Caledonian pinewood. While some species were shared between the Caledonian and plantation pinewoods (e.g. *Cychus caraboides*) others were found only in the plantations (e.g. *Carabus problematicus*). Managed forests such as these, therefore, have an intrinsic biodiversity value of their own as well as the potential to be managed toward a semi-natural scenario where they may support a more typical old-growth fauna (Humphrey *et al.* 1999; Jukes *et al.* 2001; Koivula *et al.* 2002).

The agricultural sites (LUU5 and 6), although separated in the ordination, were much more similar in beetle community composition to one another than to forest sites implying that these agricultural landscapes support a more homogenous fauna with few rare and many common, abundant species. Carabid communities in these agricultural locations are associated with mull soils, indicative of the rapidly fluctuating environment of a rotational agricultural landscape.

The mosaic sites (LUU 3 and 4) show greater heterogeneity in the beetle community composition, containing elements of the assemblages from the structurally more simple landscapes (e.g. samples from plantation stand in LUU3 contain very similar beetle assemblages to samples from the plantation site: LUU2). Therefore, for some samples in these mosaic landscapes there appears to be more concordance in species composition between than within sites. Over and above these similarities between management units the amount of birch woodland and increasing plant species richness in the mosaic landscapes is significantly associated with the beetle assemblages therein. Birches, the dominant deciduous tree in N.E. Scotland and common features of agricultural landscapes, undoubtably act as reserves of biodiversity (Kennedy and Southwood 1984, Woodcock *et al.* 2003) but increasing intensification of use both by grazing and logging (Woodcock *et al.* 2003) may have consequences for insect biodiversity in these woodland fragments.

3.4.3 Conservation relevance

Initially, it may be tempting to conclude from our data that the replacement of forest systems with intensive rotational agricultural systems would be beneficial for carabid biodiversity. This, however, would be an oversimplification as it fails to consider that biodiversity conservation is not only a question of maximising the number of species but also the composition of the community is important. For example, in agricultural landscapes many larger bodied species (e.g. *Carabus* spp. see Appendix I) are completely absent or much less common. These species are among the longest lived among the Carabidae, with a 2-year generation time, slow growing soil-dwelling larvae and apterous adults, and consequently are more vulnerable to the rapid and drastic changes that occur in these intensively managed sites (Cole *et al.* 2002). One other explanation may be changes in food resources; it has been suggested that *Carabus* and other larger carabid species prefer larger prey (e.g. Homoptera: Cicadellidae) that tend to be found in the more structurally diverse vegetation of unimproved grasslands (Lang *et al.* 1999; Cole *et al.* 2002). The retention of areas of low intensity management - heather moor, semi-natural grassland, planted and semi-natural woodlands - on farms would possibly mitigate these negative effects by providing a refuge for *Carabus* and other larger bodied species of conservation importance (Petit & Usher 1998; Koivula *et al.* 2002; de la Pena *et al.* 2003).

Our data indeed imply that woodland and forest specialists such as *Carabus* spp., *Pterostichus oblongopunctatus* and *Cychrus caraboides* are able to persist in agricultural landscapes provided sufficient areas of plantation and/or semi-natural fragments are in juxtaposition to the agricultural land (e.g. LUU4, see Appendix I) (Koivula *et al.* 2002; de la Pena *et al.* 2003). The size, degree of fragmentation and intensity of management of these woodland fragments is, however, likely to be important to certain species. For example, *P. oblongopunctatus*, a species with restricted national distribution (Hyman & Parsons 1992), generally recorded from broad-leaf semi natural woods (in this study the majority of specimens were recorded from semi-natural or managed pinewood habitats), was most abundant in LUU1 – possibly the preponderance of dead wood, continuous habitat, and lack of disturbance over time making Caledonian pinewood the favoured habitat.

3.5 Conclusions

Our data did not support the hypothesis that carabid diversity would follow the intermediate disturbance hypothesis – diversity was elevated at the more frequently disturbed agricultural sites. A possible explanation for this pattern was these agricultural habitats support ruderal carabid species (e.g. granivorous *Amara*) that respond positively to ephemeral, but abundant crops, and possibly due to fine-scale heterogeneity not measured in this study. Ordination analyses supported our second prediction that different landscape configurations would support different carabid communities and thus carabid beetles do reliably signal land-use type. Furthermore, the mosaic landscapes in this study supported the least clearly defined carabid community. Species assemblages found in these more heterogeneous landscapes were more similar to assemblages from different sites but under the same land-use – suggesting, at the landscape scale, land-use type and not heterogeneity may be the more important influence.

Caution should be exercised if attempting to generalise from the response to anthropogenic perturbation of a single taxon to the response of wider biodiversity as species are likely to respond differently to any perturbation; a consequence of the spatial scale at which the species (or higher taxon) interacts with the perturbation. Staphylinid beetles, for example, would probably be distributed differently along the land-use gradient - as they are predominantly saproxylic in their habitat association – but would be sensitive to disturbance at similar scales to carabids (< 1 ha – 1 km^2), while resident birds may respond to habitat fragmentation at much greater scales, depending on species (< 1 km^2 – 10 km^2). The lack of stratification in our sampling design meant that certain microhabitats, landscape features and possibly species were not sampled; consequently our results demand appropriate caution. Nevertheless while small-scale heterogeneity, certainly important to the diversity of carabid beetle assemblages (Niemela *et al.* 1996; Judas *et al.* 2002), was not explicitly accounted for in our sampling design, our study adds to increasing evidence that landscape-scale patterns in land-use affect carabid community structure producing distinct assemblages (Kinnunen *et al.* 2001; Ostman *et al.* 2001; Judas *et al.* 2002; Weibull *et al.* 2003).

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CHAPTER 4

LANDSCAPE STRUCTURE, PLANT DIVERSITY AND RESOURCES STRUCTURE SOIL FAUNA DIVERSITY ALONG A LAND-USE INTENSIFICATION GRADIENT [b]

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Large-scale patterns in land-use have consequences for species turnover and persistence. Changes in habitat cover and heterogeneity, plant diversity and resource (litter) quantity along a landscape scale, land-use intensification gradient are hypothesised to correlate to variation in soil animal diversity (collembola, lumbricid worms). The proportion of forest along the gradient showed a significant hump-shaped relationship with collembola and lumbricid species richness, and lumbricid abundance, peaking where landscapes were a forest-agricultural mosaic. Collembola abundance decreased while lumbricid numbers increased in spatially patchy landscapes, and a diversity of habitats increased lumbricid species richness. Above-ground diversity was correlated with below-ground diversity: collembola species richness was positively correlated with tree species richness, while lumbricid species richness and abundance was related to the diversity of forbs. Collembola abundance was positively and lumbricid abundance negatively correlated to the amount of plant litter on the soil surface and to the acidity of the soil. Anthropogenic landscape patterns in the extent and heterogeneity of habitats, the diversity of plant functional groups and variation in litter resources and soil acidity combine to structure soil animal diversity and facilitate a shift in dominance between soil micro- and macrofauna. Heterogeneity in land-use intensity at large spatial scales generates patterns in diversity among species that operate at much finer spatial scales.

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4.1 Introduction

Land-use intensification by altering the extent (Fahrig 1997; Didham *et al.* 1998a; Kruess & Tscharntke 2000; Steffan-Dewenter 2003), spatial configuration (Kruess & Tscharntke 1994; Kareiva & Wennergren 1995; Golden & Crist 1999) and context (Steffan-Dewenter *et al.* 2002; Kruess 2003; Thies *et al.* 2003) of habitat patches in anthropogenic landscapes can affect biodiversity. Declines in species diversity are associated with forest fragmentation (Didham *et al.* 1998a; Pimm & Raven 2000; Andresen 2003), conversion to agriculture (Stork *et al.* 2003; Dunn 2004) and intensification of human land-use (Lawton *et al.* 1998; Jones *et al.* 2003; Eggleton *et al.* 2005). Such large-scale anthropogenic disturbances can create patchy landscapes providing refuges and enabling species persistence via regular dispersal from more favourable patches (Hanski 1998; Petit & Usher 1998; Holland & Fahrig 2000), or alter species diversity by driving assemblage collapse and species turnover (Didham *et al.* 1998b; Jones *et al.* 2003; Eggleton *et al.* 2005; Vanbergen *et al.* 2005).

Soil biota recycle nutrients and energy vital for primary production, in this interaction with primary producers, soil decomposers underpin the functioning of terrestrial ecosystems (Bardgett & Cook 1998; Bardgett 2002; Wardle 2002). To what extent ecosystem processes and function are dependent on biodiversity (Loreau *et al.* 2001; Tilman *et al.* 2001; Hooper *et al.* 2005) and above-ground diversity influences soils and the diversity and abundance of below-ground species (Hedlund *et al.* 2003; Wardle *et al.* 2003; Wardle *et al.* 2004; De Deyn & Van der Putten 2005) remain unanswered questions.

Variation in human land-use can govern the presence and distribution of habitats, the identity of dominant plant species and plant community diversity. Plant species identity and community diversity have direct influence on soil animals via the amount and composition of plant litter (Ponge *et al.* 1993; Hansen & Coleman 1998; Hasegawa 2002; Armbrecht *et al.* 2004; De Deyn *et al.* 2004; Salamon *et al.* 2006). Variation in plant diversity and abundance may therefore influence soil animal diversity and abundance via the resource underpinning the soil decomposer system. While the effect of variation in the diversity of plant communities on above-ground arthropod diversity is known (Siemann *et al.* 1998; Koricheva *et al.* 2000), and the linkages between above- and below-ground systems in nutrient and energy flow are undoubted (Wardle *et al.* 2004), significant correlations between plant and soil animal diversity are uncommon or idiosyncratic, and often regarded as weak (Hooper *et al.* 2000; Wardle *et al.* 2003; Armbrecht *et al.* 2004).

In this study we examine the diversity (species richness and abundance) of soil micro- and macrofauna along a large-scale, land-use intensification gradient ranging from forest to agricultural landscapes. The target soil taxa (collembola and lumbricid worms) were chosen because they are important components of the soil decomposer community and are known to respond, often differently, to the same environmental gradients in, for example, pH, moisture, organic matter and land-use (Ponge 1993; Hasegawa 2002; Wardle 2002; Sousa *et al.* 2004; Joschko *et al.* 2006; Salamon *et al.* 2006). We hypothesised that the diversity of these soil animal taxa would be correlated to changes in habitat cover and heterogeneity, above-ground diversity and resource (litter) quantity along the landscape scale gradient. We predicted that soil collembola diversity would be highest in forested areas declining monotonically as the landscapes became more agricultural, while lumbricid diversity would show the opposite pattern. Furthermore, we predicted that the diversity of these soil fauna would be related to above-ground plant diversity, but that collembola and lumbricids would correlate with different plant functional groups. Finally, as forest cover is reduced and agricultural land-use increases the decrease in the litter resource and rise in soil pH will be correlated with a decline in collembola numbers, and concomitant rise in lumbricid abundance.

4.2 Methods

4.2.1 Land-use intensification gradient

Six land-use units (LUU) representing a gradient of land-use intensification were established in Aberdeenshire, Scotland, each LUU was located no more than 10 km away from the neighbouring sites (Table 4-1). Each LUU was represented by a 1 km by 1 km landscape square visually selected according to an ideal, pre-defined set of criteria corresponding to the predominant land-use within each square: LUU1 - old-growth forest (100 %); LUU2 - managed forest (100 %); LUU3 - forest-dominated (>50 %) mosaic; LUU4 - Mixed-use mosaic (50 % forest-50 % open, agricultural habitats); LUU5 – grassland dominated (> 50 %); and LUU6 - arable dominated (>50 %). Within each LUU we sampled on a systematic grid of 16 sampling points, with each sampling point at least 200m from neighbouring points and the edge of the 1 km square, giving a distribution of points within the realised habitat proportions of each LUU (Table 4-1).

4.2.2 Soil fauna sampling

Collembola were sampled with a soil core (5cm diameter x 5cm depth) at each sampling point during the period 18 April to 23 May 2002. The soil samples were transferred to the laboratory where collembola were extracted over 14 days from the soil cores using Tullgren funnels (Hopkin 2000). The specimens were individually slide-mounted and identified to species at the Centre for Ecology and Hydrology (CEH) using standard keys (Fjellberg 1998; Hopkin 2000). At each sampling point (May 2002) a steel frame quadrat (25 x 25 x15cm deep) was forced into the ground, the litter and soil were then excavated and hand-sorted on trays for lumbricids. When soil had been excavated down to the base of the quadrat (15cm depth) 1.5 L of a 0.02% formalin solution was applied to the exposed soil surface and worms emerging over a 10 min period collected. Lumbricid worms were identified to species at The Natural History Museum, London, UK.

4.2.3 Plant sampling

Information on the composition and structure of the plant community was collected at each of the 16 sampling points within each LUU from 14 May – 12 July 2001. Plant sampling coincided with the point in the growing season of maximum plant species density. A rectangular plot of 100 m^2 (20m x 5m) was laid down around the centre of the sampling point. This rectangular plot was composed of two sets of nested sub-plots of 1, 5, 12.5, 25 and $50m^2$ within which identity and number of plant species, and the percentage cover of litter were measured. The cumulative total number of vascular plant species sampled within the $100m^2$ and the species richness of plant functional groups (trees, shrubs, forbs, graminoids) was derived from this dataset.

Table 4-1. Composition and structure of the land-use gradient

LUU[1]	Latitude-Longitude	% Cover[2]			HR[3a]	NP[3b]	Soil[4]			Litter[5]	Plant *S*[6]				
		Arable	Grassland	Forest	n	n	Humus	pH	O-horizon	%	All	Tree	Shrub	Forb	Graminoid
1	57.019057N 02.859627E	0	0	100 (16)	1	1	Podzol mor	3.9	29	36	33	3	8	8	11
2	57.047952N 02.752446E	0	0	88 (16)	2	2	Mor	3.9	9	50	32	6	5	9	9
3	57.015483N 02.690494E	0	17 (4)	65 (12)	6	7	Mor-Mull	4.3	11	26	104	13	11	51	23
4	57.068030N 02.872091E	17	31 (9)	50 (6)	7	15	Mull	5.5	2	6	115	16	11	59	25
5	57.030556N 02.810504E	35 (3)	58 (12)	7 (1)	5	11	Mull	6.2	0.1	1	71	9	5	45	12
6	57.143960N 02.810504E	52 (10)	43 (5)	2 (1)	6	10	Mull	6.2	0.1	0	70	7	4	44	13

[1] Land-use units (LUU): 1.old- growth forest 2. plantation forest 3. forest-dominated mosaic 4. mixed-use mosaic 5. pasture-dominated 6. arable-dominated. All data (except GIS) were collected from 16 sampling points (LUU4: 15 sampling points due to bar on accessing arable fields) nested within each LUU on a 1km^2 grid.

[2] Percentage cover of the major habitat types, and the distribution of sampling points (number in parentheses) within the major habitat types.

[3a] HR: habitat richness (number of habitat types) and [3b] NP: landscape patchiness (cumulative number of habitat patches, irrespective of type) of each LUU (derived from LANDSAT-IRS fused image using ArcView & FRAGSTATS).

[4] Soil parameters are average (mean of 16 sampling points) a) pH and b) the depth (cm) of the organic horizon in the soil profile per LUU

[5] Percentage cover of plant litter (mean of 16 sampling points) per LUU

[6] Sum total plant species richness (*S*) of all vascular plants and four functional groups for each LUU.

4.2.4 Landscape metrics

The landscape composition of the LUUs was assessed using remotely sensed land-cover data. Two satellite images of the study area were used, a Landsat ETM 7 multispectral image and an IRS-1C panchromatic image, to create a single fused image with a 5m spatial resolution for each LUU. A hierarchic classification system based on the CORINE biotopes database (European Environment Agency) was defined and used to interpret visually the satellite images using GIS (Arcview 3.1). This CORINE classification was used to quantify landscape patterns in the LUUs using FRAGSTATS software and to calculate landscape indices for each LUU: percentage cover of forest, habitat richness (number of habitats) and landscape patchiness (cumulative number of habitat patches irrespective of type).

4.2.5 Soil variables

Soil pH and the depth of the organic (O) horizon (mm) were determined at each sampling point using a portable pH probe (Hanna HI 9024 microcomputer, Hanna Instruments Ltd) and by excavating a pit to reveal the soil profile, respectively. Three measures of each parameter were taken at each sampling point and averaged to give the mean pH and depth of the organic horizon at the sampling point.

4.2.6 Data analysis

Plot level soil fauna data were pooled to provide sum values of collembola and lumbricid species richness and abundance at the LUU scale. Plant species richness data were summed for each LUU and with average cover of plant litter, soil pH, depth of O-horizon and landscape metrics (% forest, habitat richness, landscape patchiness) per LUU (Table 1) were used as explanatory terms in the statistical analysis. The relationship of soil faunal species richness and abundance to the components of the land-use gradient was analysed as count data within a generalised linear model (GLM) using a Poisson error structure and a Log-link function. An exact test (720 permutations) was used to determine the significance of the observed GLM model deviance (SAS Institute 1999). This test gives the exact probability that the deviance as small as that obtained by the fitted GLM model could have occurred by chance, and therefore the robustness of the correlation. Owing to the intercorrelation between the various explanatory terms and the limited degrees of freedom at this spatial scale ($n = 6$) only the univariate effect of each covariate on collembola and lumbricid species richness and abundance are reported.

4.3 Results

Both collembola and plant species richness showed a maximum peak where a mixture of forest and open habitats occurred (LUU4), conversely lumbricid worm species richness was greatest where pasture was the dominant land-use (LUU5) (Figure 4-1a). Collembola abundance peaked in the plantation forest site (LUU2) and declined as the proportion of agricultural land in the landscape increased (Figure 4-1b). Lumbricid abundance showed the opposite trend with greater numbers in the sites (LUU4-6) where a significant amount of the land-cover was devoted to agriculture (Figure 4-1b). Collembola abundance was negatively correlated with lumbricid abundance (Figure 4-1c, Table 4-2) but there was no significant relationship between lumbricid worm and collembola species richness, or between species richness and abundance of either soil taxa (Table 4-2).

4.3.1 Landscape metrics

Of the landscape parameters derived from remote sensing (Table 4-1), the proportion of forest in the surveyed landscapes showed a quadratic relationship with the species richness of collembola and lumbricids, and lumbricid abundance (Figures 4-2a-b, Table 4-2). Collembola species richness and lumbricid abundance was greatest where a mix of forested and agricultural habitats existed (LUU3 & 4, Figures 4-2a-b, Table 4-1), whereas lumbricid species richness was greatest where pasture was a major land-use (LUU5) and was lower when the landscape was predominantly forested (LUU1-3) or was dominated by intensive arable farming (LUU6) (Figure 4-2a, Table 4-1). Collembola and lumbricid species richness was positively correlated with the habitat richness (although marginally non-significant) of the landscape (Table 4-2), species richness was greatest in the mosaic landscape LUU4 where a diversity of habitats existed.

Figure 4-1. (a) Species richness (sum total) of collembola, lumbricid worms and plants, (b) abundance (sum total) of collembola and lumbricid worms, and c) relationship between collembola and lumbricid abundance along a land-use intensification gradient ranging from old-growth forest (1), plantation forest (2), forest dominated mosaic (3), mixed-use mosaic (4), pasture (5) and arable dominated (6) sites. Soil fauna and plants were sampled on a grid of 16 sampling points within each site.

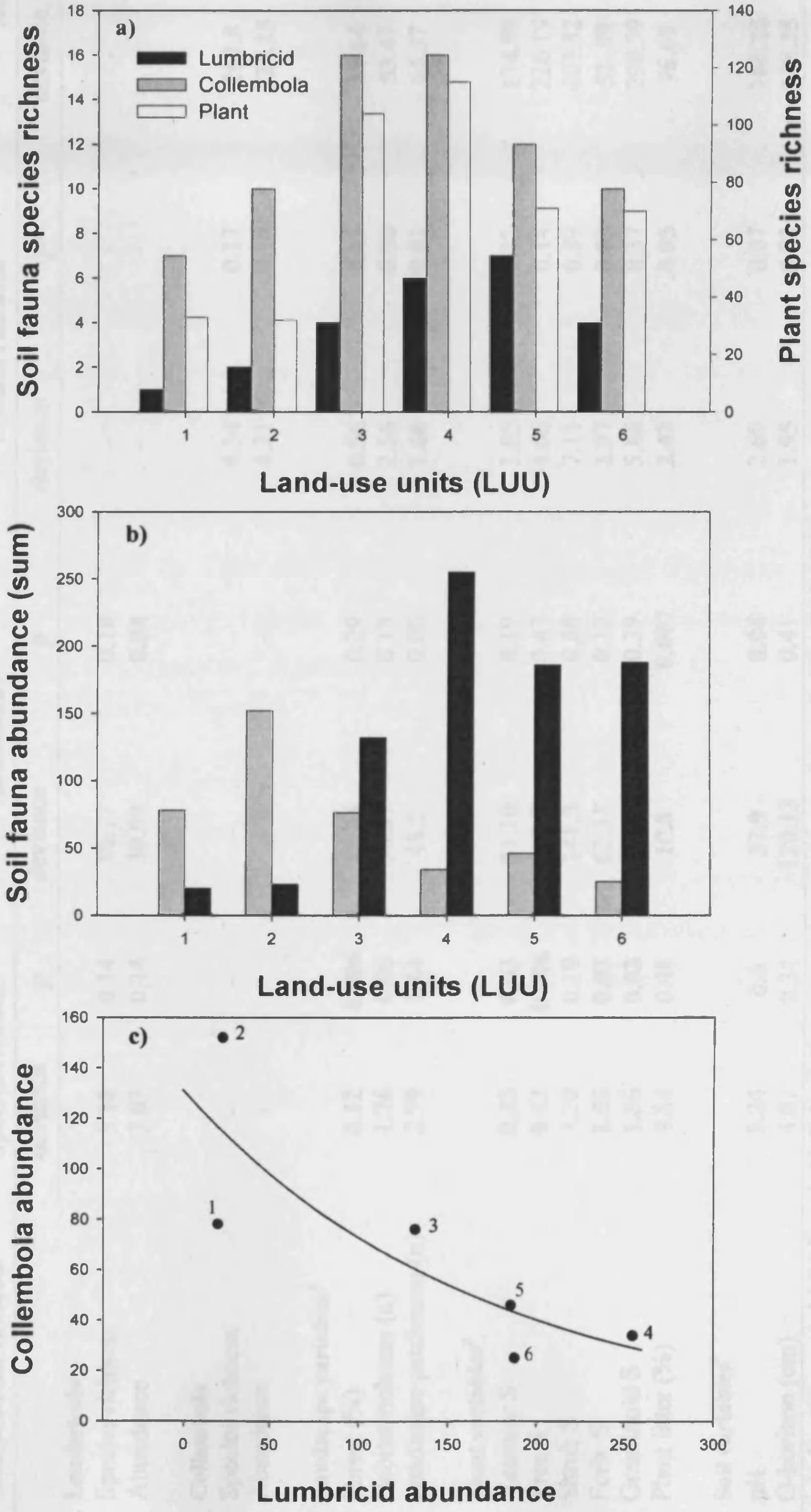


Table 4-2 Results of exact test (720 permutations) of the deviance in soil fauna species richness and abundance explained by generalised linear models (GLM) with a Poisson error distribution and Log link function (SAS).

	Collembola				**Lumbricids**			
Independent variable	**Species richness**		**Abundance**		**Species richness**		**Abundance**	
	deviance	*p*	deviance	*p*	deviance	*p*	deviance	*p*
Lumbricids								
Species richness	3.18	0.14	80.77	0.18	-	-	-	-
Abundance	3.03	0.14	**30.99**	**0.04**	-	-	-	-
Collembola								
Species richness	-	-	-	-	4.34	0.17	262.8	0.15
Abundance	-	-	-	-	4.21	0.14	**124.25**	**0.02**
Landscape variables[1]								
Forest (%)	**0.12**	**0.006**	56.05	0.29	**0.56**	**0.03**	**10.64**	**0.02**
Habitat richness (n)	1.76	0.06	70.87	0.13	2.56	0.06	**53.47**	**0.008**
Landscape patchiness (n)	2.99	1.44	48.5	0.06	**1.66**	**0.02**	**64.37**	**0.003**
Plant variables[2]								
Vascular S	**0.83**	**0.03**	85.10	0.19	3.85	0.12	**174.59**	**0.05**
Tree S	**0.43**	**0.006**	119.0	0.47	4.06	0.14	226.19	0.10
Shrub S	3.20	0.19	141.3	0.88	7.11	0.89	403.32	0.68
Forb S	**1.55**	**0.03**	62.31	0.12	**1.97**	**0.03**	**52. 99**	**0.01**
Graminoid S	**1.36**	**0.03**	112.9	0.39	5.86	0.37	290.59	0.17
Plant litter (%)	4.84	0.48	**10.8**	**0.007**	**2.42**	**0.05**	**96.69**	**0.01**
Soil variables[3]								
pH	5.24	0.6	**37.9**	**0.04**	2.69	0.07	**168.25**	**0.04**
O-horizon (cm)	4.01	0.31	120.13	0.41	**1.95**	**0.03**	**138.35**	**0.03**

[1] derived for each LUU from LANDSAT-IRS fused image using ArcView & FRAGSTATS;

[2] Sum total species richness (*S*) of vascular plants and functional groups and mean percentage cover of litter. Data collected from 16 sampling points nested within each LUU on a 1km^2 grid;

[3] Soil pH and the depth of the organic horizon in the soil profile. Data analysed are means of 16 sampling points nested within each LUU on a 1km^2 grid

Collembola and lumbricid worm abundance were both significantly related to the spatial patchiness of the landscape with the collembola numbers negatively and worm numbers positively correlated to landscape patchiness (Figure 4-2c, Table 4-2). Collembola numerically dominate the forest-dominated sites, in particular the plantation forest (LUU2), whereas lumbricids were more abundant in the more heterogeneous landscapes, particularly LUU4 (Figure 4-2c). Lumbricid worm species richness was also positively related to the overall patchiness of the landscape (Table 4-2).

4.3.2 Plant functional group diversity

Collembola species richness was more closely related to the richness of the plant assemblage than to soil variables (Figure 4-3a, Table 4-2). When the plant assemblage diversity was divided by functional groups, it was the species richness of trees that was the most significant correlate of observed collembola species richness (Figure 4-3a); other significant plant community covariates included the species richness of forbs (Figure 4-3b) and graminoids, but not shrubs (Table 4-2). Lumbricid worm species richness and abundance was not related to tree diversity; the species richness of forbs was the most significant plant assemblage correlate of worm abundance and species richness (Table 4-2, Figure 4-3b).

4.3.3 Soil variables

While collembola species richness was best explained by forest cover and above-ground plant diversity, the abundance of collembola was significantly correlated with edaphic factors. The decline in the average percentage cover of plant litter along the gradient as agricultural areas replaced forest elements of the landscape was strongly correlated with the reduction in collembola abundance (Figure 4-4a, Table 4-2).

Figure 4-2. The observed (lumbricids: open symbols, collembola: closed symbols) and fitted - dashed (lumbricids) and solid (collembola) lines from GLM with Poisson error distribution - relationships along a land-use intensification gradient in Scotland between (a) collembola and lumbricids species richness, (b) lumbricid abundance and the proportion of forest cover, c) collembola and lumbricid abundance and landscape patchiness, and d) lumbricid abundance and habitat richness. Symbol labels indicate LUU number and predominant land-use: (1) old-growth forest, (2) plantation forest, (3) forest dominated mosaic, (4) mixed-use mosaic, (5) pasture and (6) arable dominated.

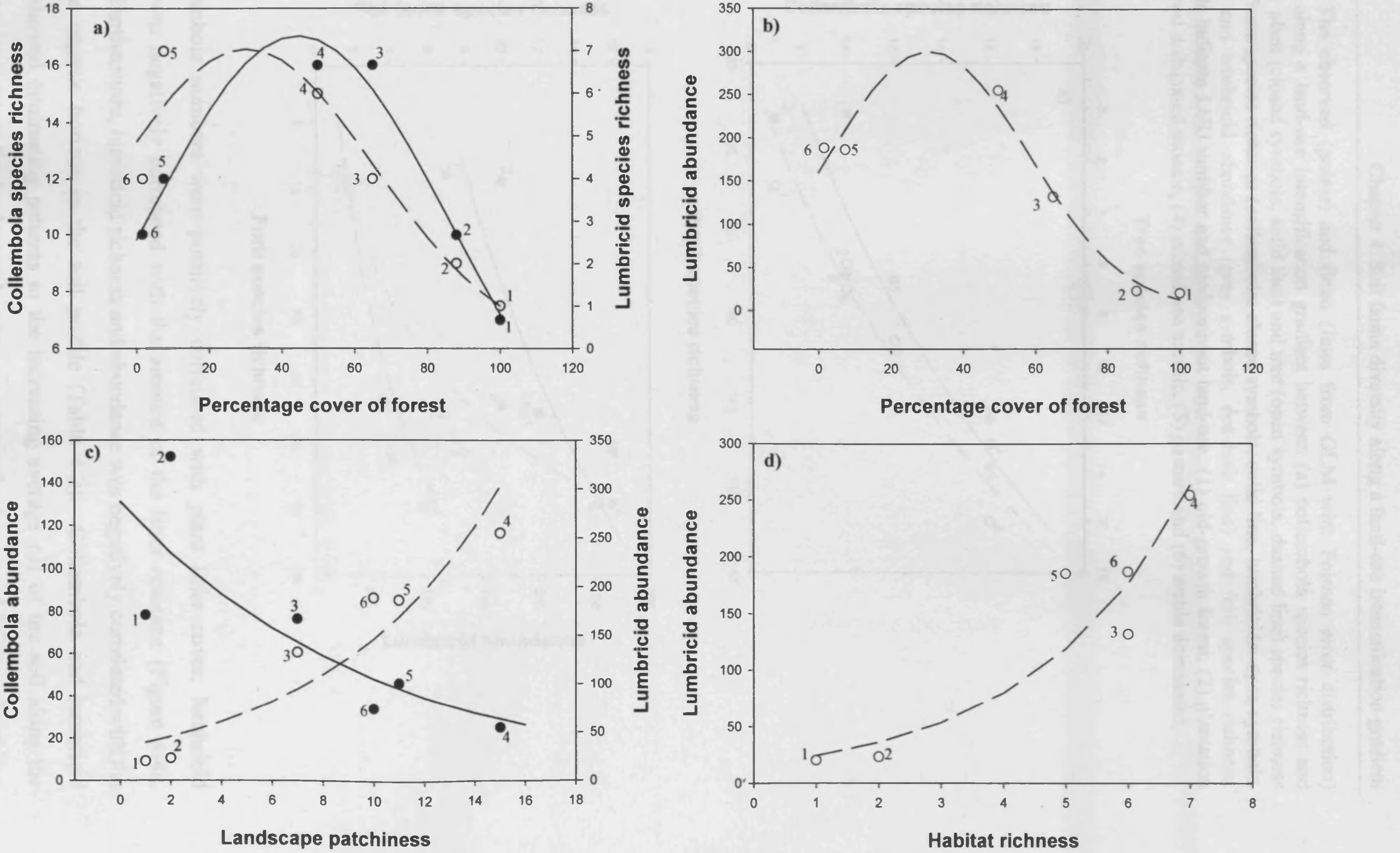
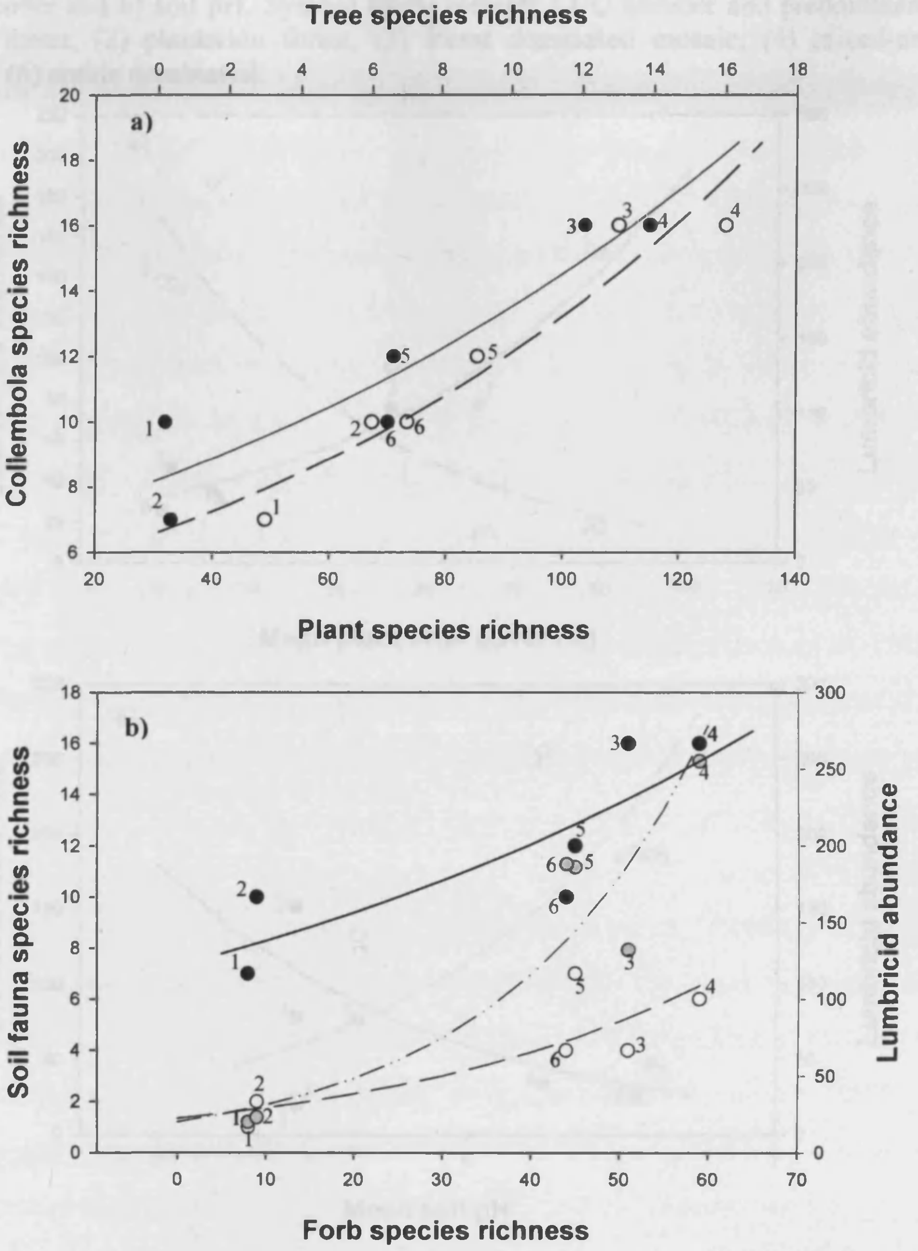
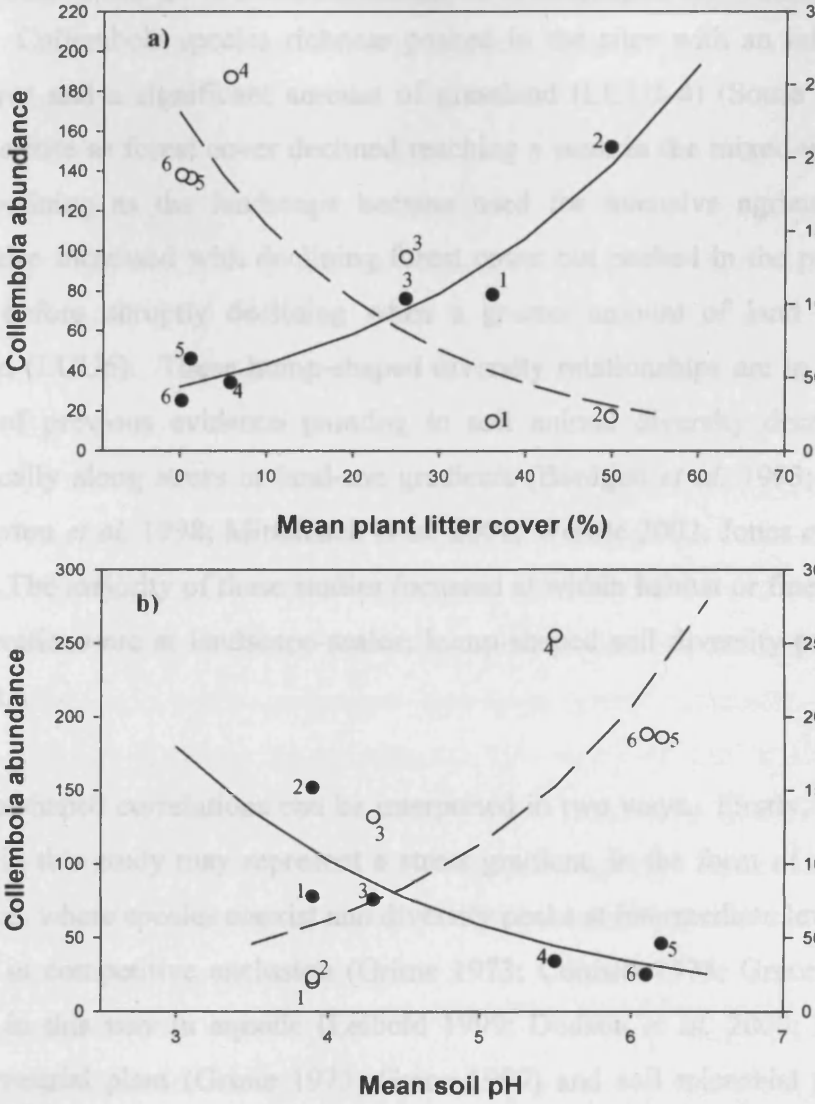


Figure 4-3. The observed (points) and fitted (lines from GLM with Poisson error distribution) relationships along a land-use intensification gradient between (a) collembola species richness and total vascular plant (closed symbols, solid line) and tree (open symbols, dashed line) species richness and (b) soil fauna species richness (collembola: closed symbols, solid line, lumbricids: open symbols, dashed line) and lumbricid abundance (grey symbols, dot-dash line) and forb species richness. Symbol labels indicate LUU number and predominant land-use: (1) old-growth forest, (2) plantation forest, (3) forest dominated mosaic, (4) mixed-use mosaic, (5) pasture and (6) arable dominated.



While collembola numbers were positively correlated with plant litter cover, lumbricid abundance was negatively correlated with the amount of the litter resource (Figure 4-4a, Table 4-2). Furthermore, lumbricid richness and abundance was negatively correlated with the depth of the organic horizon in the soil profile (Table 4-2). Collembola and lumbricid abundance showed contrasting patterns to the increasing average pH of the soil along the intensification gradient as the landscape became progressively dominated by more intensive agriculture. Collembola numbers were lower in the landscapes where there was a significant agricultural presence and soil pH more neutral, whereas lumbricid abundance was lower under forest soils and acidic conditions (Figure 4-4b, Table 4-2).

Figure 4-4. The observed (lumbricids: open symbols, collembola: closed symbols) and fitted - dashed (lumbricids) and solid (collembola) lines from GLM with Poisson error distribution - relationships along a land-use intensification gradient between collembola and lumbricid abundance and mean (a) plant litter cover and b) soil pH. Symbol labels indicate LUU number and predominant land-use: (1) old-growth forest, (2) plantation forest, (3) forest dominated mosaic, (4) mixed-use mosaic, (5) pasture, and (6) arable dominated.



4.4 Discussion

Changes in habitat cover and heterogeneity led to changes in the species richness and abundance of both collembola and lumbricid worms. Contrary to our prediction that collembola diversity would decline and worm diversity increase as the landscape became less forested we found that the species richness of collembola and lumbricids, and lumbricid abundance had a hump-shaped relationship with the proportion of forest along the land-use gradient. Collembola species richness peaked in the sites with an intermediate amount of forest cover and a significant amount of grassland (LUU3-4) (Sousa *et al.* 2006). Worm abundance rose as forest cover declined reaching a peak in the mixed-use landscape (LUU4) before declining as the landscape became used for intensive agriculture. Worm species richness also increased with declining forest cover but peaked in the pasture dominated site (LUU5), before abruptly declining when a greater amount of land was used for arable production (LUU6). These hump-shaped diversity relationships are in direct contrast to the majority of previous evidence pointing to soil animal diversity decreasing or increasing monotonically along stress or land-use gradients (Bardgett *et al.* 1993; Freckman & Ettema 1993; Lawton *et al.* 1998; Mittelbach *et al.* 2001; Wardle 2002; Jones *et al.* 2003; Maraun *et al.* 2003). The majority of these studies focussed at within habitat or finer spatial scales, while our observations are at landscape-scales; hump-shaped soil diversity patterns may be scale-dependent.

The hump-shaped correlations can be interpreted in two ways. Firstly, the land-use gradient surveyed in this study may represent a stress gradient, in the form of resource limitation or disturbance, where species coexist and diversity peaks at intermediate levels of the stress via a reduction in competitive exclusion (Grime 1973; Connell 1978; Grace 1999). Diversity is governed in this way in aquatic (Leibold 1999; Dodson *et al.* 2000; Horner-Devine *et al.* 2003), terrestrial plant (Grime 1973; Grace 1999) and soil microbial (Degens *et al.* 2001) communities; evidence for such unimodal relationships between stress or disturbance and terrestrial animal diversity remains more elusive, particularly so for soil faunal diversity (Mittelbach *et al.* 2001; Wardle 2001, 2002). Secondly, it is recognised that habitat spatial heterogeneity can contribute to species coexistence and persistence (Levin & Paine 1974; Ellner *et al.* 2001). The spatial patchiness of the landscapes arising from human land-use (Ettema & Wardle 2002) may enable populations to persist in habitat refuges, and to act as a source habitat facilitating repeated colonisation of more unfavourable areas of the landscape

(Hanski 1998; Ellner *et al.* 2001). In this way spatially heterogeneous landscapes may produce the highest diversity at a given point.

For hump-shaped patterns to be generated by the existence of a stress gradient would require competitive exclusion to be occurring between the soil taxa. In the current study, although collembola and lumbricid abundance were negatively correlated, there was little other evidence of competitive interactions between these taxa, and in the absence of empirical data we reject the intermediate disturbance hypothesis as an explanation for the observed hump-shaped patterns in soil faunal diversity.

A more likely explanation is that the hump-shaped soil diversity patterns are a property of the extent of forest habitat, and spatial heterogeneity of the landscape arising from human land-uses (Eggleton *et al.* 2005; Sousa *et al.* 2006). Differences do however exist between the two taxa. Collembola species richness was strongly correlated to the extent of forest habitat with peak richness occurring where a mix of forest and open habitats co-occur. This peak in collembola diversity may arise because elements of forest and agricultural communities persist in this heterogeneous habitat mosaic, and through repeated colonisation of habitat sinks from adjacent source habitats. Lumbricid diversity was more strongly correlated with landscape spatial heterogeneity: landscapes with a diversity of habitat types had greater lumbricid abundance, while landscapes with high spatial patchiness contained both more worm species and numbers of individuals. The effect of habitat diversity may provide alternative niches while spatial patchiness may provide refuges. Patches of deciduous woodland or semi-permanent pasture in the more frequently disturbed agricultural areas of LUU4, 5 and 6 may, for example, allow worm populations to persist undisturbed in otherwise intensively tilled agricultural landscapes.

The soil fauna may not be responding directly to the land-use gradient but, instead, be correlated with changes in plant diversity along that gradient. The observed peak in soil faunal diversity in the heterogeneous landscapes would then be due to the corresponding peak in plant diversity at that point. Previous studies have shown that above-ground consumer and plant diversity can be significantly correlated (Siemann *et al.* 1998; Koricheva *et al.* 2000) and that plant species identity can have an effect on soil diversity and trophic structure (Wardle *et al.* 2003; De Deyn *et al.* 2004). Few studies have shown significant correlations between plant and below-ground diversity (Hooper *et al.* 2000; Wardle 2002; De Deyn *et al.* 2004; Ponge *et al.* 2005).

Faunal species richness was positively correlated with the diversity of the above-ground vegetation. The identity of the plant functional group to which soil faunal diversity was correlated varied, however, with the identity of the soil taxa. Collembola species richness was correlated to overall vascular plant diversity, the species richness of graminoids and forbs, but it was mostly variation in tree species richness along the gradient that was highly correlated with collembola diversity. Lumbricid species richness and abundance was, by contrast, positively correlated only with forb species richness. This finding confirms those of previous experimental work that show the importance of plant identity (in this case functional group identity) for soil animal diversity (Wardle *et al.* 2003; De Deyn *et al.* 2004), but also highlights the role of species diversity within plant functional groups in structuring soil animal diversity at large spatial scales.

The positive effect of tree species richness on collembola diversity further explains the hump-shaped relationship with forest cover, since the peak at intermediate forest cover (LUU3 and 4) is coincident with the greatest tree species richness. The forest sites LUU1 and 2 (100 & 80% forest cover respectively) are totally dominated by coniferous trees (mainly *Pinus sylvestris*), while the heterogeneous mosaic sites (LUU3 & 4: 65-50% forest cover) include individuals and patches of deciduous tree species (*Quercus sp.& Betula sp.*). This greater diversity of tree species at the gradient mid-point may facilitate the observed peak in the species richness of the collembola by producing heterogeneity in the availability and quality of the litter resource, thereby enabling collembola species coexistence in the more diverse resource space (Hansen & Coleman 1998; Hansen 2000).

Forest cover and tree species had a further bottom-up effect on soil fauna abundance via the amount of litter resource available to decomposers and the soil acidity of these sites. As predicted the decline in the amount of tree litter, as coniferous forest cover in the landscapes was reduced, had a significant and contrary effect on the abundance of the studied soil animal taxa. Collembola abundance was positively and lumbricid worm numbers negatively correlated with the reduction of litter cover on the soil surface as forest cover was replaced by agriculture along the land-use gradient. Collembola and worm abundance also showed an inverse response to the gradient in soil pH with differing land-use types: as the landscape became less forested the soil pH rose and this was correlated with a rise in lumbricid worm and concomitant decline in collembola numbers. The decline in tree litter inputs and acidity along the gradient marks the transition in the soil decomposer community from acidophilic, arthropod dominated soils to soils that are more neutral and dominated by lumbricid worms (Eggleton *et al.* 2005).

This study is among the first (Eggleton *et al.* 2005; Sousa *et al.* 2006) to demonstrate a hump-shaped relationship of soil animal diversity to a land-use intensification gradient. It appears that a number of interrelated factors operating at different ecological scales (landscape, habitat, plant) are involved in structuring spatial patterns in soil faunal diversity. Human land-use generates coarse patterns in the extent (forest cover) and heterogeneity (patchiness) of habitats, identity and diversity of plant functional groups, and variation in litter resources and soil acidity. These factors combine to structure soil animal assemblages facilitating species turnover and shifts in dominance between different soil micro- and macrofauna (Eggleton *et al.* 2005). It is not explicit from these data if this variation in diversity is partly generated by individual species responding to stress gradients (e.g. soil acidity) within the overall land-use gradient. Experimental study is needed to tease apart the relative importance of the factors correlated with diversity in this snapshot of these soil animal communities; whether competitive interactions occur between collembola and lumbricids at fine-scales, and if this can scale up to produce larger-scale diversity patterns which are stable over time. These data do, however, imply that varying human land-use intensity at large spatial scales can generate patterns in diversity among species that operate at much finer spatial scales.

Acknowledgements

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CHAPTER 5

PREDATORS FAIL BUT HERBIVORES PREVAIL: A CONSEQUENCE OF ANTHROPOGENIC DISTURBANCE TO A NATURALLY PATCHY HABITAT [c]

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Tertiary trophic levels (predators, parasitoids) are known to be more sensitive than secondary trophic levels (herbivores) to anthropogenic disturbance. Using a naturally fragmented habitat we studied the influence of habitat area and disturbance (cattle introduction) on the diversity of invertebrate trophic guilds (herbivores, omnivores, predators). Habitat area had no influence on the species richness or abundance of the trophic guilds. The presence of cattle led to a reduction in the diversity (species richness and abundance) of secondary consumers, but primary consumers were unaffected. This loss of secondary consumers meant grazed habitat supported fewer trophic levels compared with ungrazed habitat. Cattle modify the habitat producing a compositionally diverse but architecturally simple plant assemblage distinct from the ungrazed situation. The lower diversity of secondary consumers in grazed habitat was correlated with this grazing-dependent habitat heterogeneity, while primary consumers were unaffected. Our findings support the suggestion that tertiary trophic levels are more vulnerable than herbivores to the effects of anthropogenic disturbance, in this case cattle grazing. The undisturbed semi-natural habitat provides a refuge for invertebrate predators; the disturbance of this habitat has potential consequences for pest suppression in adjacent agricultural land and regional biodiversity.

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[c] Submitted to Oecologia February 2006

5.1 Introduction

The greater rarity and population variability of tertiary trophic levels (predators, parasitoids) makes them more sensitive (i.e. greater extinction probability, decreased diversity and abundance) than secondary trophic levels (herbivores) to anthropogenic disturbance (Kruess & Tscharntke 1994; Didham *et al.* 1998a; Didham *et al.* 1998b; Gilbert *et al.* 1998; Spencer 2000). This differential impact of anthropogenic disturbance according to trophic position has been shown to occur in fragmented habitats (Didham *et al.* 1998b; Gilbert *et al.* 1998; Davies *et al.* 2000; Komonen *et al.* 2000; Kruess & Tscharntke 2000); in landscapes varying in structure and land-use (Tscharntke *et al.* 2002; Thies *et al.* 2003; Purtauf *et al.* 2005); where the presence of livestock perturbs semi-natural habitat (Vanbergen *et al.* 2006); and where grazing intensity is high (Cagnolo *et al.* 2002; Kruess & Tscharntke 2002). These anthropogenic effects impact negatively on secondary consumers (predators, parasitoids) both directly via habitat changes and indirectly mediated by their prey (Thies *et al.* 2003; Vanbergen *et al.* 2006).

The majority of studies that have examined the differential impact of disturbance on different trophic levels centre around examples of habitat fragmentation as consequences of human land-use (Didham *et al.* 1998b; Davies *et al.* 2000; Gibb & Hochuli 2002) or experimentation (Kruess & Tscharntke 1994; Gilbert *et al.* 1998; Golden & Crist 1999; Kruess & Tscharntke 2000). Some studies have explored the influence of natural habitat patchiness on natural enemy attack rates (Brodmann *et al.* 1997; Doak 2000) and others the effect of disturbance to natural habitats on parasitism rates (Vanbergen *et al.* 2006) but none, to our knowledge, have examined the impact of anthropogenic disturbance to a naturally fragmented habitat on the diversity of tertiary trophic levels.

This study exploits naturally fragmented lowland birch woodlands that are, in some cases, semi-natural habitat under no human management while in other cases are used as part of the surrounding agricultural land-use - cattle production (Armstrong *et al.* 2003; Woodcock *et al.* 2003; Vanbergen *et al.* 2006). Livestock grazing is a common anthropogenic disturbance of habitats and ecosystems with profound consequences for plant populations and community diversity (Hobbs 1996; Rambo & Faeth 1999; Fowler 2002; Pykala 2003), and the presence and diversity of consumer species dependent, either directly or indirectly, on the plant assemblage (Gibson *et al.* 1992a; Borges & Brown 2001; Kruess & Tscharntke 2002; Hartley *et al.* 2003; Woodcock *et al.* 2005). The presence and absence of cattle grazing in disjunct woodland patches therefore represented a serendipitous experiment to test whether disturbance to a naturally fragmented habitat has a differential effect on invertebrate diversity (species richness and abundance) according to trophic position.

We hypothesised that tertiary trophic levels (secondary consumers), of the woodland understorey arthropod assemblage, would be more sensitive than secondary trophic levels (primary consumers) to both woodland patch area and disturbance from cattle grazing. A number of specific predictions were tested: i) the species richness and abundance of arthropods and feeding guilds (herbivore, omnivore, predator) would be greater in larger and/or ungrazed woodland patches; ii) secondary consumers (omnivore, predator) would show a comparatively greater reduction in diversity (species richness and abundance) than primary consumers (herbivore) in smaller and cattle-grazed woodlands; iii) cattle grazing would modify the birch habitat creating a more diverse, compositionally and structurally distinct plant assemblage compared to the ungrazed situation; and iv) the observed reduction in arthropod and feeding guild diversity would be correlated with this grazing-dependent habitat heterogeneity.

5.2 Method

5.2.1 Sites and experimental design

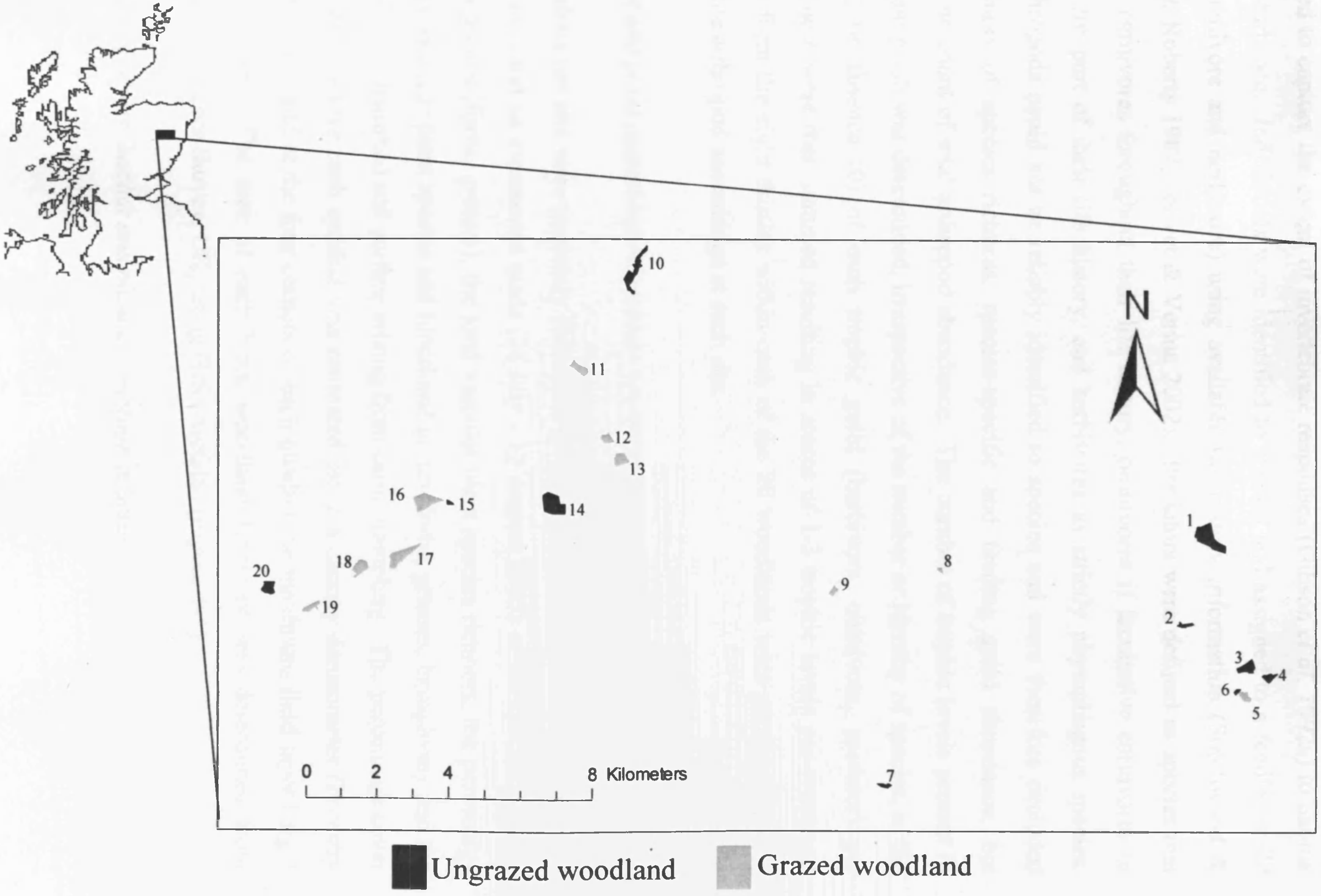
Birches (*Betula spp.* L.), a pioneer species supporting great diversity of associated insects (Kennedy & Southwood 1984), provide a refuge for forest-dependent species (Petit & Usher 1998; Woodcock *et al.* 2003) and are the dominant deciduous forest type in Northern Scotland. 20 birch woodland sites were selected in the Deeside region of Aberdeenshire (57°3.0'N, 2°30.2'E - 57°3.3'N, 2°57.9'E) according to the presence ($n = 10$) or absence ($n = 10$) of livestock grazing. This management had been in place for at least the preceding 10 years. Care was taken to ensure that sites selected were not geographically confounded (Figure 5-1). Livestock in the grazed sites were predominantly cattle ($n = 10$), although occasional additional low level grazing by sheep ($n = 3$) and horses ($n = 1$) did occur. The low incidence of grazing by wild ungulates (i.e. roe deer) was not measured because it was assumed to be of minimal importance when compared with the intensive livestock management. No other systematic management (e.g. forestry) occurred at the sites. At the end of April 2003 (coincident with the date of birch budburst) eight second-year *Cirsium* *palustre* (Linnaeus) thistles were transplanted, from two nearby sites, into each of the woodland locations (160 thistles in total).

As thistles are known to support a large and diverse insect fauna, and attract both herbivores and their predators, these plants were used as trap plants to sample arthropods that were associated directly with pre-existing populations of *C. palustre* or with the wider birch habitat. Within each site the eight thistles were randomly planted within a 4 x 4 grid (15m^2), with each point on the grid separated by 5m. The centre of the grid was situated at least 50m from the woodland edge. Prior to flowering cattle trampling destroyed some replicate thistles (18 %), and neighbouring thistles of local origin were used as replacements. No evidence of direct vertebrate grazing on experimental thistles was seen during the course of this experiment.

Plate 5.1. Balnagowan farm: a grazed birch woodland

Plate 5.2. Auchattie: an ungrazed birch woodland

Figure 5-1. Schematic map showing the location of the study area in Scotland (black rectangle) giving the name, distribution (West-East) and area (ha) of grazed and ungrazed birch woodland fragments used in this study.



Site	Area (ha)
1. Brathens	28.30
2. Blackhall	2.46
3. Scolty	8.87
4. Auchattie	4.95
5. Beechgrove	4.75
6. Sunnydale	1.05
7. Woodend	2.54
8. Potarch	1.17
9. Allancreich	2.86
10. Woodfield	16.97
11. Bridgend	8.01
12. Balnagowan hill	4.57
13. Balnagowan farm	8.96
14. Airfield	26.28
15. St. James	1.31
16. Dinnet	18.98
17. Nertherton	21.81
18. Corntulloch	11.26
19. Greystone	4.91
20. Braehead	8.36

5.2.2 Arthropod sampling

Each thistle was sampled (13-16 July 2003) for 2 minutes with a motorised suction sampler (McCulloch BVM240™) and the arthropods collected in an Organza™ gauze bag. Multiple arthropod taxa (Heteroptera, Coleoptera, Auchenorrhyncha, Araneae) known to be sensitive to grazing (Gibson *et al.* 1992a; Gardner *et al.* 1997; Hartley *et al.* 2003; Woodcock *et al.* 2005) were sampled to capture the extent of invertebrate responses (Gibson *et al.* 1992a) to habitat area and disturbance. Individuals were identified to species and assigned to a feeding guild (predator, omnivore and herbivore) using available life-history information (Southwood & Leston 1959; Roberts 1987; Jolivet & Verma 2002). Predators were defined as species that are obligate carnivores throughout their life history, omnivores if facultative carnivores or carnivorous for part of their life history, and herbivores as strictly phytophagous species. Juvenile arthropods could not be reliably identified to species and were therefore excluded from all counts of species richness, species-specific and feeding guild abundance, but included in the count of total arthropod abundance. The number of trophic levels present in each woodland patch was determined, irrespective of the number or identity of species, as the presence (1) or absence (0) of each trophic guild (herbivore, omnivore, predator) per woodland. These were then summed resulting in scores of 1-3 trophic levels per woodland patch. Data from the eight thistles within each of the 20 woodlands were pooled to give a snapshot of the arthropod assemblage at each site.

5.2.3 Habitat and plant assemblage variables

Six 1m^2 quadrats per site were randomly placed on grid points not occupied by experimental thistle replicates, and an assessment made (28 July - 12 August 2003) of the species richness of functional groups (forbs, grasses), the total vascular plant species richness, the percentage cover for each vascular plant species and functional group (forbs, grasses, bryophyte), and the proportion of bare, disturbed soil surface arising from cattle trampling. The percentage cover of the tree canopy above each quadrat was estimated using a canopy densiometer (Forestry Suppliers Inc. USA) and at the four corners of each quadrat the maximum field layer height (mm) was recorded. The area of each birch woodland fragment was determined from digitised maps (Ordnance Survey, UK) using GIS (ArcGIS) (Figure 5-1).

5.2.4 Statistical analysis: habitat and plant assemblage structure

Wilcoxon signed-rank tests were used to test if mean habitat variables differed between grazed and ungrazed sites. Factors responsible for the structuring of the plant assemblages were identified using redundancy analysis (RDA, CANOCO version 4.5); this is a constrained form of principal components analysis (PCA) that identifies trends in the scatter of species data that are linearly related to a set of constraining, explanatory variables. RDA was used to relate the percentage cover of vascular plant species to measured environmental variables (canopy density, sward height, proportion of bare and trampled soil, bryophyte and plant litter cover). Variables derived from the plant species data (forb and grass percentage cover, vascular plant species richness) were fitted as supplementary variables to illustrate further trends in the plant assemblage and did not affect the variance explained by the RDA of the vascular plant assemblage. The significance of the explanatory variables in structuring the plant assemblage was determined with a forward selection procedure using Monte-Carlo tests constrained within sites (9999 permutations). Thus the model presented is a partial redundancy analysis (pRDA) controlling for site-level variance when assessing the impact of grazing-dependent habitat variation on the plant assemblage.

5.2.5 Statistical analysis: arthropod and feeding guild species richness and abundance

Untransformed counts of total arthropod, herbivore, omnivore and predator populations per site were used as the dependent variables in generalised linear models (GLM, SAS v.8.02, SAS Institute) using a Poisson error distribution with a Log-link function. Firstly, arthropod and feeding guild species richness and abundance were correlated to the area of the woodland and the presence or absence of cattle. Following on, the categorical term 'cattle presence' was replaced with continuous grazing-dependent habitat variables, namely median values of vascular plant, forb and grass species richness, mean cover (%) of functional groups (forbs, grasses, bryophytes), mean tree canopy density (%), bare, trampled soil (%), mean sward height (mm) and the coefficient of variation ($s/\bar{x}$) in sward height.

Inter-correlation between habitat variables (Appendix II) meant the separation of their effects on the invertebrate assemblage by step-wise multivariate regression was confounded. Principal components analysis (PCA) was performed on these habitat covariates. The orthogonal axes scores of the first three principal components (which are uncorrelated with each other, but principally correlated with specific habitat variables) were then used as the explanatory variables in the GLM model. This PCA step reduced the number of explanatory variables to sets of co-varying habitat variables, allowing the influence of orthogonal habitat gradients on the insect abundance to be tested. Simplification of multivariate GLM was by step-wise elimination of the least significant term (PCA axes 1-3) until the most parsimonious model was found; χ^2 values of explanatory terms using adjusted sums of squares are reported.

Analysis of deviance was performed to assess whether the addition of the categorical term 'cattle presence' to a model containing the significant continuous habitat variables (e.g. PCA axes scores) resulted in a significant increase in the explained deviance of the model, and therefore whether there was a residual effect of cattle presence on arthropod diversity over and above the significant grazing-dependent habitat variation identified in the PCA analysis.

5.3 Results

5.3.1 Influence of woodland area and cattle presence on arthropods

A total of 874 individuals were identified from 56 invertebrate species (Appendix III). The Heteroptera were the most abundant taxon (388 individuals, 14 species), followed by the Araneae (369, 12), the Auchenorrhyncha (83, 11) and the Coleoptera (38, 19). Species accumulation curves are asymptotic in grazed woodland and close to asymptotic in the ungrazed habitat indicating the sampling method produced a representative sample of invertebrate species richness in the birch habitats (Figure 5-2). Despite considerable variation in woodland size (Figure 5-1) the area of the woodland patch did not affect significantly the species richness or abundance of either all arthropods or the feeding guilds (Table 5-1). Our data do not support the prediction that the larger woodland patches would support greater arthropod and functional group diversity. Furthermore the prediction that secondary consumers would suffer a comparatively greater loss of diversity than primary consumers in smaller habitat patches was not upheld by these data.

Figure 5-2. Species accumulation curves by number of samples for grazed and ungrazed birch woods. Dotted lines are species richness ± SD. Plots constructed using Estimate S.

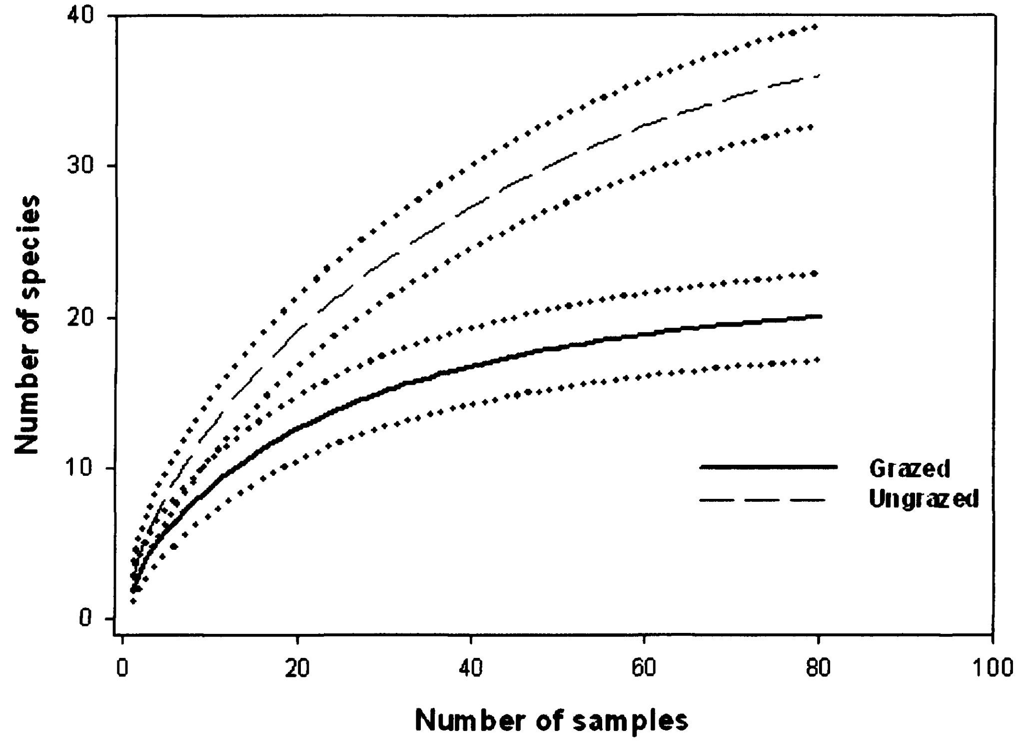
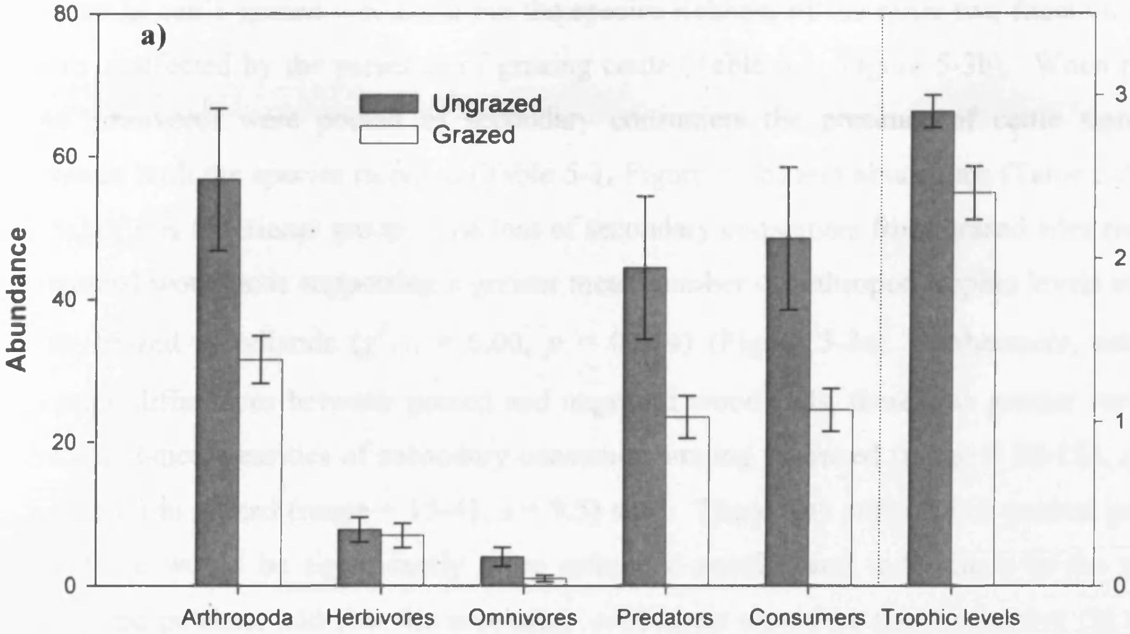
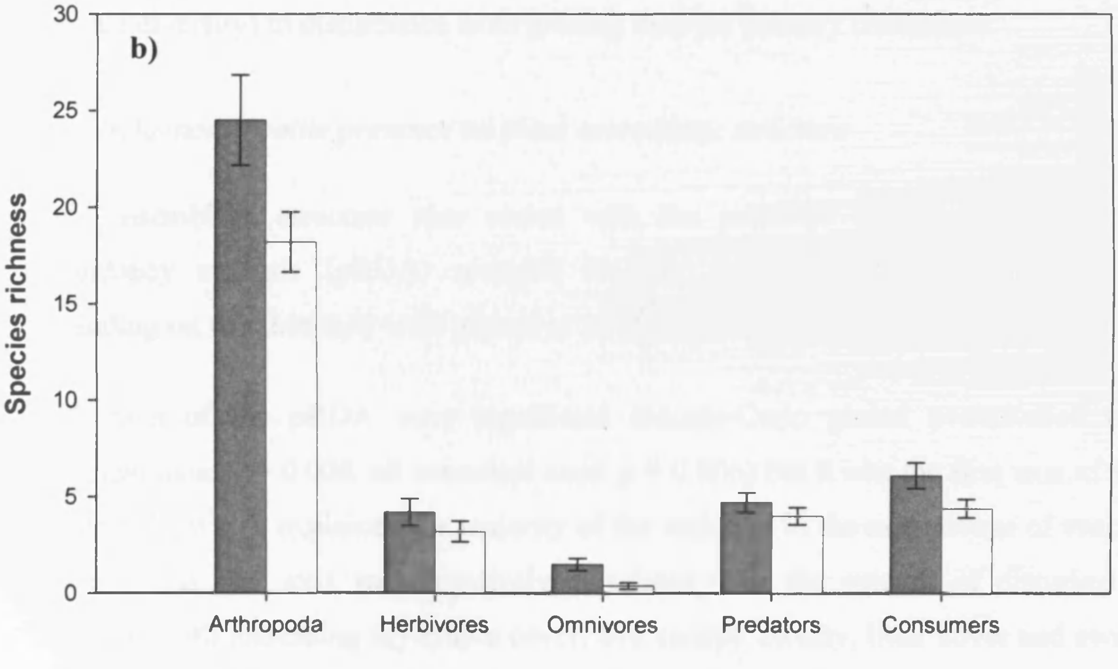


Table 5-1. Summary of generalised linear models (GLM) of the influence of habitat area and cattle presence on the arthropod assemblage. Counts of individuals and species were modelled with Poisson error distribution and Log-link function.

	Woodland area (ha)				**Cattle presence**			
	estimate	df	χ^2	*P*	estimate	df	χ^2	*P*
Species Richness								
Arthropoda	-0.00	1,17	0.69	0.41	**-0.35**	**1,17**	**4.49**	**0.03**
Herbivores	-0.00	1,17	0.46	0.50	-0.28	1,17	1.30	0.25
Omnivores	-0.00	1,17	0.72	0.39	**-1.34**	**1,17**	**10.43**	**0.001**
Predators	-0.00	1,17	0.38	0.54	-0.17	1,17	1.11	0.29
2° Consumers	-0.00	1,17	0.78	0.38	**-0.35**	**1,17**	**4.91**	**0.03**
Abundance								
Arthropoda	0.00	1,17	1.61	0.20	**-0.56**	**1,17**	**6.82**	**0.009**
Herbivores	-0.00	1,17	0.50	0.58	-0.18	1,17	0.31	0.58
Omnivores	-0.00	1,17	0.66	0.42	**-1.43**	**1,17**	**6.46**	**0.01**
Predators	0.00	1,17	2.75	0.10	**-0.59**	**1,17**	**5.04**	**0.02**
2° Consumers	0.00	1,17	2.33	0.13	**-0.64**	**1,17**	**6.87**	**0.009**

Figure 5-3. The effect of the presence of cattle grazing in woodlands on the a) abundance and b) species richness of Arthropoda, feeding guilds (herbivore, omnivore and predator), and all secondary consumers (predators and omnivores). The number of trophic levels present in grazed and ungrazed woodlands is also shown on a secondary y-axis. Data are mean counts ± SE derived from 10 grazed and 10 ungrazed woodlands. Data were analysed with generalized linear models (SAS) using Poisson errors and a Log-link function.





Cattle grazing, however, did influence the composition and abundance of the invertebrate assemblage. Total arthropod densities and species richness were greatest in the ungrazed birch woods (Table 5-1, Figure 5-3). The total abundances of invertebrate predators and omnivorous insects were greater in the ungrazed woodlands while total herbivore abundance was unaffected (Table 5-1, Figure 5-3a). The species richness of the omnivore guild was greater in cattle-grazed woodland but the species richness of the other two functional groups were unaffected by the presence of grazing cattle (Table 5-1, Figure 5-3b). When predators and omnivores were pooled as secondary consumers the presence of cattle significantly lowered both the species richness (Table 5-1, Figure 5-3b) and abundance (Table 5-1, Figure 5-3a) of this functional group. The loss of secondary consumers from grazed sites resulted in ungrazed woodlands supporting a greater mean number of arthropod trophic levels compared with grazed woodlands ($\chi^2_{1,17}$ = 6.00, p = 0.014) (Figure 5-3a). Furthermore, aside from average differences between grazed and ungrazed woodlands, there was greater variation in the population densities of secondary consumers among ungrazed (range = 20-124, s = 31.5) compared to grazed (range = 15-41, s = 9.5) sites. These data support our general prediction that there would be significantly more arthropod species and individuals in the ungrazed woodland patches, and that the secondary consumers would be more sensitive (in terms of reduced diversity) to disturbance from grazing than the primary consumers.

5.3.2 Influence of cattle presence on plant assemblage structure

Plant assemblage structure also varied with the presence of grazing livestock; partial redundancy analysis (pRDA) revealed a clear separation between plant assemblages depending on whether they were grazed or not (Figure 5-4).

Both axes of the pRDA were significant (Monte-Carlo global permutation tests: first canonical axis: p = 0.008, all canonical axes: p = 0.006) but it was the first axis of the pRDA (Table 5-2), which explained the majority of the variation in the assemblage of vascular plant species. This first axis was negatively correlated with the amount of disturbed soil and positively with increasing bryophyte cover, tree canopy density, litter cover and sward height (Table 5-2, Figure 5-4). Overall the plant assemblages in the grazed sites tended to be more speciose, with a greater proportion of forb cover and of the soil surface disturbed and unvegetated by cattle trampling, lower levels of bryophyte cover, tree canopy density, and reduced levels of plant litter and mean sward height compared to the ungrazed plant assemblages (Tables 5-2 & 5-3, Figure 5-4). Our third prediction that cattle would modify the habitat producing a more diverse, compositionally and structurally distinct plant assemblage compared to the ungrazed situation was therefore supported.

Figure 5-4. Partial redundancy analysis (pRDA) of plant assemblages from 10 grazed and 10 ungrazed birch woodlands. Significant environmental variables structuring the plant assemblage are represented by solid line vectors: tree canopy density (Canopy), plant litter (Litter) and bryophyte (Bryo) percentage cover, mean height (mm) of ground vegetation (Sward), and the percentage cover of bare, disturbed soil (Bare). Supplementary variables are derived from the plant assemblages and represented by dashed line vectors: total vascular plant species richness (Plant S), percentage cover of plant functional groups (Forb and Grass). The species scores of the 10 most abundant (percentage cover) plant species are shown (in rank order: *Holcus lanatus* (Ho.la.), *Agrostis capillaris* (Ag.ca.), *Pteridium aquilinum* (Pt.aq.), *Holcus mollis* (Ho.mo.), *Poa trivialis* (Po.tr.), *Agrostis stolonifera* (Ag.st.), *Molinia caerulea* (Mo.ca.), *Deschampsia flexuosa* (De.fl.), *Ranunculus ripens* (Ra.re.), *Trifolium ripens* (Tr. Re.). Open and closed symbols denote the mean sample scores per site SE. Significance of environmental variables was determined using a forward selection procedure with Monte-Carlo permutation (9999) tests.

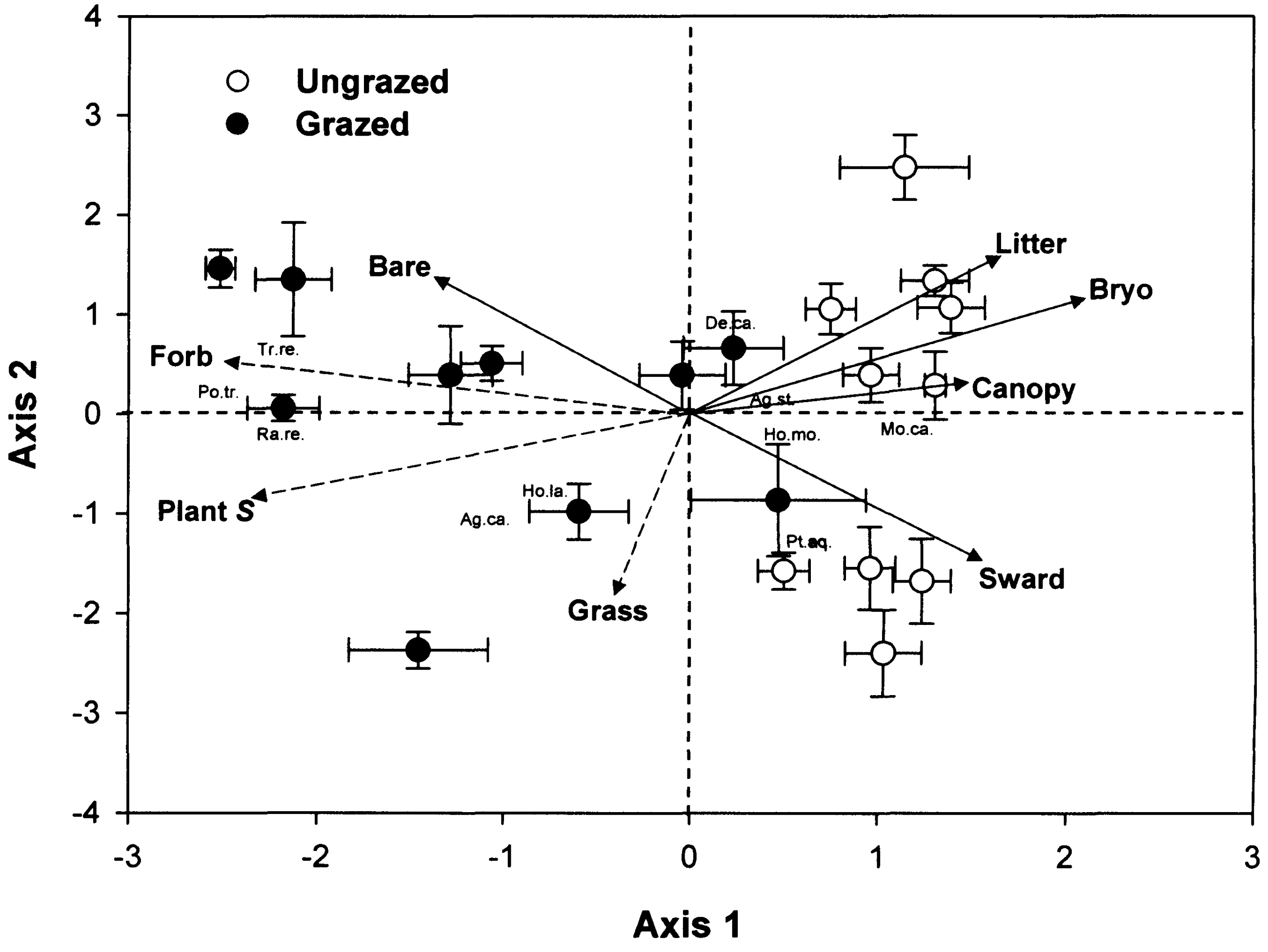


Table 5-2. Partial redundancy analysis (pRDA) of plant species cover data with Monte-Carlo tests constrained by site (9999 permutations). Correlation coefficients of significant environmental variables to ordination axes are shown. Eigenvalues are a measure of the relative dispersion of species scores on each ordination axis and therefore the relative importance of each axis. Supplementary variables are fitted passively and do not affect the ordination.

Axes	**1**	**2**	**3**	**Total variance**
Eigenvalues	0.08	0.03	0.01	1.000
Species–environment correlation	0.72	0.65	0.61	
Cumulative percentage variance				
of species data	7.6	10.6	12.1	
of species-environment relation	55.2	76.8	87.8	
Sum of all eigenvalues				0.98
Sum of all canonical eigenvalues				0.14
Intra-set correlation coefficients				
Environmental variables				**Monte-Carlo**
Bryophyta (%)	0.71	0.48	-0.23	0.004
Bare ground (%)	-0.56	0.50	0.37	0.04
Sward (mm)	0.50	-0.54	0.66	0.04
Canopy (%)	0.56	0.04	-0.37	0.003
Litter (%)	0.56	0.40	0.19	0.02
Supplementary variables				
Forb (%)	-0.86	0.27	-0.05	-
Grass (%)	-0.08	-0.84	-0.97	-
Plant *S* (n)	-0.79	-0.41	-0.16	-

Table 5-3. Wilcoxon signed-ranks comparison of averages of plant and habitat variables from grazed (n =10) and ungrazed (n =10) woodland sites.

Variable	**Mean**		**SD**		**z**	**P**
	Grazed	Ungrazed	Grazed	Ungrazed		
Plant species richness	26.3	16.8	6.3	5.1	2.88	0.002
Grass species richness	7.4	6.0	1.8	1.9	1.34	0.09
Forb species richness	15.5	6.4	4.1	3.9	3.41	0.0003
Bare ground (%)	18.0	1.2	0.1	0.0	2.82	0.002
Sward height (mm)	347.1	503.8	161.7	176.1	-1.85	0.03
Sward height (CV)	178.0	134.2	58.9	72.8	1.55	0.06
Grasses (%)	76.9	76.0	14.1	30.7	-0.57	0.285
Forbs (%)	42.6	13.7	20.1	8.6	3.21	0.0007
Bryophytes (%)	7.3	26.0	7.3	6.6	-2.83	0.002
Canopy density (%)	63.0	87.4	0.3	0.1	-1.70	0.04
Area (ha)	8.73	10.12	6.85	10.25	0.11	0.45

5.3.3 Effect of grazing-dependent habitat heterogeneity on arthropods

The PCA of habitat variables revealed that the first three axes summarised 74 % of the habitat variation across grazed and ungrazed birch woodlands. The first PCA axis (38 % of variation) was positively associated with increasing total vascular plant and forb species richness, and forb percentage cover and so represented a gradient in flowering plant diversity. The second and third PCA axes summarised the architectural and spatial complexity of the plant assemblage: the second axis (22 %) was positively associated with average sward height, grass species richness and percentage cover; while the third axis (14 %) was positively related to spatial variability in sward height, quantified by the coefficient of variation. These three principal components effectively summarised grazing-dependent habitat variability and were, as predicted, significant correlates of arthropod and functional group diversity.

Total arthropod species richness was negatively related to the third principal component, correlated with spatial variability in sward height (PCA 3), but not to the other gradients (PCA 1 & 2) in habitat heterogeneity (Table 5-4). Arthropod abundance was negatively related to the first PCA axis - correlated with increasing plant, forb richness and forb percent cover - and positively related to the second principal component - associated with grass richness, percent cover and sward height (Table 5-4). Herbivore species richness and abundance were not significantly affected by the grazing-dependent habitat variation summarised in the PCA axes (Table 5-4). The omnivore guild was, however, negatively associated with the first principal component axis (plant and forb richness, forb cover) both in terms of the number of species and the number of individuals (Table 5-4, Figure 5-5c). Species richness of the predator guild was not significantly affected by grazing-driven habitat variation (Table 5-4). Predator abundance was positively related to the second axis of habitat variation (sward height, grass species richness and cover) (Table 5-4, Figure 5-5d) but only marginally and negatively with the first principal component (plant and forb richness, forb cover) (Table 5-4). When predators and omnivores were pooled as secondary consumers the species richness of this functional grouping was negatively related to the third principal component (Table 5-4, Figure 5-5e), correlated with the spatial variability in the height of the sward, while secondary consumer abundance was negatively related to the first (plant and forb richness, forb cover) and positively to the second PCA axis (sward height, grass species richness and cover) (Table 5-4, Figure 5-5a-b).

Furthermore, analysis of deviance revealed that the change in deviance explained by the models including both cattle presence/absence and significant habitat (PCA) variables did not differ significantly from the model where only the habitat variables were included (Abundance: Arthropod $F_{1,16} = 2.03, p = 0.17$; Predator $F_{1,17} = 1.62, p = 0.22$; Omnivore $F_{1,16} = 0.97, p = 0.34$; Secondary consumers $F_{1,16} = 1.99, p = 0.18$; Species richness: Omnivore $F_{1,17} = 2.96, p = 0.10$; Secondary consumers $F_{1,17} = 3.40, p = 0.09$). Thus there was no additional grazing effect, above that encompassed by the PCA of the measured habitat variables on the diversity of the arthropod guilds.

Our fourth prediction that a reduction in arthropod and guild diversity would be correlated to grazing-dependent habitat heterogeneity was strongly supported. Herbivorous insects were unaffected by cattle-driven changes to the plant community but, correlated to a loss of vegetation height and a concomitant increase in flowering plant diversity, there was a reduction in secondary consumer diversity in the grazed birch woods.

Table 5-4. Effect of grazing-dependent habitat heterogeneity on arthropod and feeding guild species richness and abundance. Summary of generalised linear models (GLM) using the first three axes scores of habitat covariates (from PCA) as independent variables. Counts of individuals and species were modelled with Poisson error distribution and Log-link, χ^2-values adjusted to account for other significant independent variables in the model. Habitat covariates contributing the most variance to the PCA axes are given in parentheses.

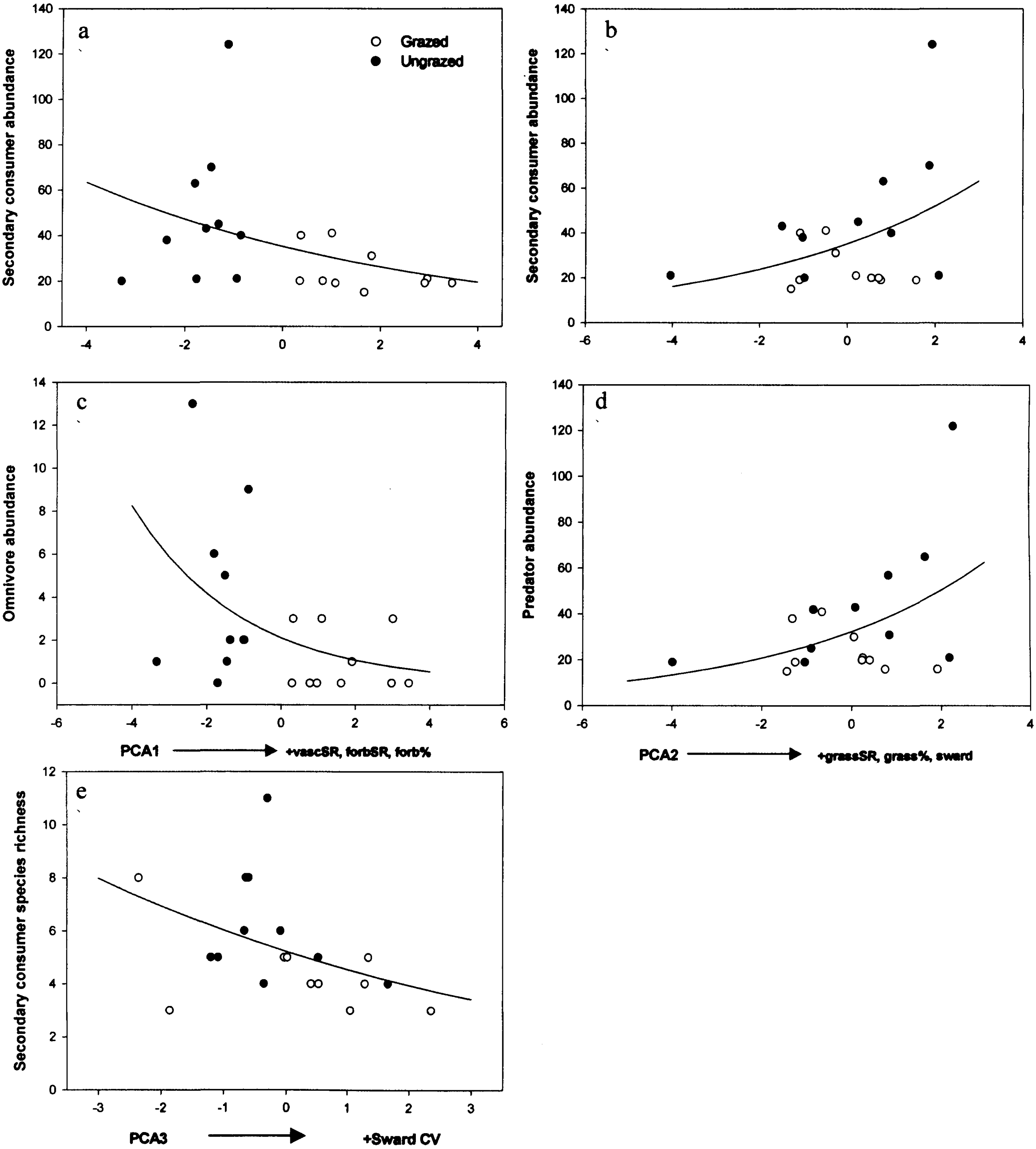
	PCA1 (+ vascSR, forbSR, forb%)[1]				PCA2 (+sward, grassSR, grass%)[2]				PCA3 (+swardCV)[3]			
	estimate	df	χ^2	*P*	estimate	df	χ^2	*P*	estimate	df	χ^2	*P*
Species Richness												
Arthropoda	-0.06	1,16	2.87	0.09	0.10	1,17	3.38	0.07	**-0.15**	**1,18**	**4.60**	**0.03**
Herbivores	-0.06	1,16	1.17	0.28	0.15	1,18	3.09	0.08	-0.16	1,17	3.15	0.08
Omnivores	**-0.27**	**1,18**	**5.52**	**0.02**	0.04	1,16	0.08	0.78	-0.31	1,17	2.35	0.12
Predators	-0.01	1,16	0.11	0.74	0.09	1,17	3.24	0.07	-0.11	1,18	3.10	0.08
2° Consumers	-0.05	1,16	2.02	0.15	0.07	1,17	1.73	0.19	**-0.14**	**1,18**	**4.28**	**0.04**
Abundance												
Arthropoda	**-0.13**	**1,17**	**5.01**	**0.02**	**0.16**	**1,17**	**5.17**	**0.02**	-0.63	1,16	0.44	0.51
Herbivores	-0.05	1,16	0.36	0.55	0.07	1,17	0.44	0.55	-0.20	1,18	2.52	0.11
Omnivores	**-0.34**	**1,18**	**5.40**	**0.02**	0.14	1,16	0.60	0.44	-0.45	1,17	2.94	0.09
Predators	-0.13	1,17	3.44	0.06	**0.19**	**1,17**	**4.41**	**0.03**	-0.00	1,16	0.00	0.97
2° Consumers	**-0.15**	**1,17**	**4.86**	**0.03**	**0.18**	**1,17**	**4.40**	**0.03**	-0.03	1,16	0.09	0.76

[1] vascSR, forbSR, forb% – total vascular plant, forb species richness and forb percentage cover

[2] sward, grass SR, grass% – mean sward height, grass species richness and percentage cover

[3] swardCV – spatial variability (CV^2) in sward height

Figure 5-5. The relationship between the number of individuals in the (a) secondary consumer ($\chi^2_{1,17} = 4.86$, $p = 0.03$) and (c) omnivore guild ($\chi^2_{1,18} = 5.40$, $p = 0.02$) and the first principal component (vascular plant, forb species richness and forb cover), and (b) secondary consumer ($\chi^2_{1,17} = 4.40$, $p = 0.03$) and (d) predator ($\chi^2_{1,17} = 4.41$, $p = 0.03$) abundance and the second principal component (sward height, grass species richness and cover). The relationship between the species richness of (e) secondary consumers ($\chi^2_{1,18} = 4.28$, $p = 0.04$) and the third principal component (CV sward height). Symbols are the total number of individuals in grazed (open circles) and ungrazed (closed circles) woodlands (n=10 ungrazed, 10 grazed). Lines were fitted using GLM with Poisson error distribution and log link (SAS).



5.4 Discussion

The presence of grazing cattle led to a reduction in both species richness and abundance of the arthropod assemblage. This impact of grazing on invertebrate diversity depended on trophic position: the abundance and species richness of secondary consumers was significantly lower where cattle were present, whilst the primary consumers were unaffected. This loss of facultative and obligate predators led to grazed woodlands supporting, on average, fewer trophic levels compared to the ungrazed situation. Higher trophic levels of the arthropod assemblage were, as predicted, more sensitive to the presence of grazing livestock.

Cattle in this woodland system act as ecosystem engineers (Hobbs 1996; Jones *et al.* 1997) influencing the arthropod assemblage by modifying the habitat and altering plant assemblage structure. Grazing shifted the woodland plant community from one characterised by few species (including disturbance sensitive bryophytes) with an architecturally complex sward (dominated by *Molinia caerula* L. (Moench), *Pteridium aquilinum* (L.) Kuhn, *Holcus* L. *spp*), to one characterised by increased plant and forb diversity, greater cover of forbs, lower vegetation height and higher levels of disturbance to the soil surface. These data suggest that cattle through a combination of trampling and grazing suppressed competitive-dominants and created niche space (Grant *et al.* 1996; Fowler 2002). The ungrazed plant assemblage tended to be dominated by competitively superior plant species (e.g. *Molinia caerula*, *Pteridium aquilinum, Holcus spp.*). Grazing reduced the cover of these competitive-dominants (Grant *et al.* 1996; Humphrey & Swaine 1997; Pakeman 2004) and increased the cover of grazing tolerant species (e.g. *Ranunculus repens* L., *Trifolium repens* L., *Poa trivialis* L.). These grazing-dependent changes were significantly correlated to the lower species richness and abundance of secondary consumers, supporting our prediction that grazing-dependent habitat heterogeneity would negatively affect the tertiary trophic level.

Our data lead us to suggest that the shift in plant species composition led to a loss of architectural complexity in the understorey plant assemblage, and thus a reduction in the amount and diversity of niches in grazed woodlands available to arthropod predators (Gibson *et al.* 1992b; Kruess & Tscharntke 2002). Web-building spiders, for example, are a predatory group dependent on rigid plant structures to anchor webs and are therefore sensitive to losses in vertical structure due to grazing (Gibson *et al.* 1992b). Furthermore, cattle tend to graze unevenly in space (Armstrong *et al.* 2003) and this did create greater horizontal variability (quantified by the coefficient of variation) in sward height in the grazed habitat. This greater spatial heterogeneity was also correlated with a decline in the species richness of secondary consumers, and thus, for the taxa sampled, does not compensate for the overall loss of vertical structure and associated niches in the sward. Without a controlled experiment, however, where habitat structure is directly manipulated the precise mechanism governing the loss of higher trophic levels in these habitats remains equivocal.

As well as the mean difference between the grazed and ungrazed woodlands in species richness and abundance of secondary consumers there was greater variation in population densities of secondary consumers among the samples from ungrazed sites compared with among grazed locations. This implies that the habitat modification by cattle led not only to a reduction in the average abundance and species richness of arthropod secondary consumers, but also to a truncation in the potential range of predator population densities that these semi-natural habitat patches can support.

Woodland area did not affect either species richness or abundance of the arthropod assemblage, or those of the feeding guilds. This was unexpected given the published evidence for the effect of habitat area on species persistence and diversity (Kareiva & Wennergren 1995; Fahrig 1997; Didham *et al.* 1998a; Andresen 2003; Steffan-Dewenter 2003). The absence of a species-area relationship does not appear to be an artefact of the sampling method as species accumulation curves imply that the majority of species in both the grazed and ungrazed habitat were captured. A more extensive sampling strategy over time may, however, have revealed the predicted species-area relationship and whether the loss of secondary consumers from grazed woodlands is irrevocable.

Our findings support earlier studies that show tertiary trophic levels to be more vulnerable than herbivores to the effects of anthropogenic disturbance (Didham *et al.* 1998b; Davies *et al.* 2000; Kruess & Tscharntke 2002; Purtauf *et al.* 2005). Specifically we show that grazing cattle can lead to losses of predatory species from semi-natural habitat, analogous to species losses due to habitat loss and fragmentation in other systems (Didham *et al.* 1998b; Gilbert *et al.* 1998; Davies *et al.* 2000). Few studies have looked at the effect of anthropogenic grazing in semi-natural habitat on trophic guild diversity (Cagnolo *et al.* 2002), or the impact of grazing on tertiary trophic levels in a naturally fragmented woodland habitat (Vanbergen *et al.* 2006). In this birch woodland system anthropogenic grazing is a greater influence on diversity than habitat area, particularly for the tertiary trophic level. Cattle introductions affected both primary and tertiary trophic levels (but not invertebrate herbivores) shifting plant and invertebrate diversity from a typical birch wood scenario to a typical grazed grassland assemblage.

This study provides an insight into the importance of livestock grazing for arthropod trophic structure, pest management and regional biodiversity. Natural habitat patches, such as woodlands and hedgerows, have been shown to act as refuges for insect predators from agricultural disturbance, contributing to the population persistence of predators, and thereby improving their impact on pest populations (Petit & Usher 1998; Ostman *et al.* 2001; Marshall & Moonen 2002; Thies *et al.* 2003). The use of these natural woodland patches for agricultural grazing may have negative consequences for the sustainable biological control of insect pests in adjacent agricultural land. Grazing livestock in primary and secondary semi-natural forest is known to affect invertebrate diversity (Bromham *et al.* 1999), mutualistic (Vazquez & Simberloff 2003) and antagonistic (Vanbergen *et al.* 2006) interactions. This paper demonstrates that the potentially high contribution - due to the regionally large area covered by these birch woods (Woodcock *et al.* 2003) - of these secondary woodland patches to regional biodiversity is, depending on trophic position, both promoted (plants) and eroded (invertebrates) by their use for livestock production. Maintaining a balance between livestock production and biodiversity conservation (i.e. the number of these semi-natural woodlands used for grazing should be offset against those set-aside) would produce at a regional level a mosaic of management and habitats allowing biodiversity and economic needs to coexist.

Livestock grazing is often used as part of nature reserve management in Europe to promote restoration of habitats and species conservation (WallisDeVries & Raemakers 2001; Armstrong *et al.* 2003; Pykala 2003; Poyry *et al.* 2004). Such grazing management regimes are frequently targeted at desired plant communities (Bokdam & Gleichman 2000; Pykala 2003) and associated Lepidoptera populations (WallisDeVries & Raemakers 2001; Poyry *et al.* 2004), and it is the impact of the management on these target groups that are measured. This study and others (Gardner *et al.* 1995; Evans *et al.* 2005; Woodcock *et al.* 2005) show that livestock grazing can alter habitat structure with direct, negative consequences for populations of secondary consumers. There should, therefore, be more consideration for the consequences of conservation grazing on non-target species, and particularly tertiary trophic levels, as it could lead to changes in the trophic structure of the community. Monitoring of biodiversity restoration measures should encompass a diverse range of taxa and trophic levels to assess accurately the ramifications of conservation grazing for the structure of the wider food-web.

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CHAPTER 6

CONSEQUENCES FOR HOST-PARASITOID INTERACTIONS OF GRAZING-DEPENDENT HABITAT HETEROGENEITY [d]

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Environmental heterogeneity can produce effects that cascade up to higher trophic levels and affect species interactions. We hypothesised that grazing-dependent habitat heterogeneity and grazing-independent host plant heterogeneity would directly and indirectly influence a host-parasitoid interaction in a woodland habitat. Thistles were randomly planted in 20 birch woodlands, half of which are grazed by cattle. The abundances of two species of seed herbivore and their shared parasitoid were measured, and related to habitat and host-plant heterogeneity. The presence of cattle grazing created a structurally and compositionally distinct plant assemblage from the ungrazed semi-natural situation. Grazing did not affect the number or dispersion of the host plant underpinning the host-parasitoid interaction. The density of one insect herbivore, Tephritis conura, *and its parasitoid* Pteromalus elevatus *was significantly increased by the presence of cattle; but another herbivore,* Xyphosia miliaria, *was unaffected. Percent parasitism of* T. conura *was increased in grazed habitat occurring at twice the rate found in ungrazed habitat. The increase in* T. conura *abundance was correlated with increased species richness and cover of forbs in grazed sites. This effect of grazing-dependent habitat variation on host insect density cascaded up to parasitoid density and percent parasitism. Habitat heterogeneity had a further direct, positive effect on parasitoid density and percent parasitism after controlling for host insect density. Independent of grazing, heterogeneity in host plant flowering, architecture and stature further affected* T. conura *and its parasitoid's densities. Parasitoid density was also affected by the dispersion of the host plant. A combination of habitat and host-plant scale environmental heterogeneity influenced a host-parasitoid interaction indirectly and directly, providing a rare example of*

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an anthropogenic disturbance positively affecting a tertiary trophic level. This finding highlights the need to consider not only the importance of bottom-up effects for top-down processes, but also the role of environmental heterogeneity arising from anthropogenic disturbance for trophic interactions like parasitism.

6.1 Introduction

Trophic cascades occur when one species (or group of species) indirectly affects a second species (or group of species) by influencing the abundance or biomass of a third, connected to the first two by trophic interactions (Rosenheim *et al.* 1993). The indirect effect of predators on plants mediated via impact on herbivore populations is one type of trophic cascade (Gomez & Zamora 1994; Moran *et al.* 1996; Schmitz 2003). Typically these studies focus on simple interaction chains (Matsumoto *et al.* 2003) or webs (Finke & Denno 2004), and examine the effect of top predators on the density or behaviour of other predators (Rosenheim *et al.* 1993; Lang 2003) and herbivores (Krivan & Schmitz 2004). Fewer studies have investigated the extent to which such relatively simple food chains may be affected by perturbation of the wider community or habitat in which the interaction chain is embedded (Chase 1996; Jones *et al.* 1997; Grabowski 2004; Preisser & Strong 2004).

Cattle can significantly alter plant communities and habitats (Hobbs 1996; Rambo & Faeth 1999). Cattle grazing can suppress competitive dominants and facilitate the emergence of a distinct, more diverse plant community (Rambo & Faeth 1999; Fowler 2002; Pykala 2003), and affect higher trophic level diversity and abundance (Gibson *et al.* 1992; Kruess & Tscharntke 2002b; Woodcock *et al.* 2005). Studies examining the effect of cattle grazing on species interactions are less common (Kruess & Tscharntke 2002; Vazquez & Simberloff 2003, 2004). Cattle grazing in Argentine forests, for example, disrupted pollinator–plant mutualism webs via the loss of a number of "keystone interactions" (Vazquez & Simberloff 2003) and for one plant species cattle-driven changes to plant population density affected plant reproduction by reducing pollen deposition by insects (Vazquez & Simberloff 2004).

Parasitism has the potential to be affected by the cascading effects of cattle ecosystem engineering (Jones *et al.* 1997; Kruess & Tscharntke 2002b) as environmental heterogeneity at both coarse (e.g. habitat) and fine scales (e.g. host plant) can affect host-parasitoid interactions. Forest fragmentation is known to influence parasitism rates (Roland & Taylor 1997); and isolated 'habitat fragments' tend to support reduced parasitoid diversity and percent parasitism compared with contiguous habitat (Kruess & Tscharntke 1994). Host-plant patch size (Sheehan & Shelton 1989; Doak 2000), patch isolation (Doak 2000), plant species identity (Roland 1986; Englishloeb *et al.* 1993) and plant architecture (Gingras & Boivin 2002; Gingras *et al.* 2003) affect both the pattern and level of parasitism. In summary, the effect of spatial and structural heterogeneity at lower trophic levels, and at different scales, can affect parasitoid density and parasitism rates.

In this present study we assess the impact of grazing by cattle in birch woodlands, and the environmental heterogeneity it generates, on a simple thistle-seed herbivore-parasitoid interaction chain. Independent of grazing effects we also evaluate the influence of host-plant heterogeneity (e.g. architecture) to this same interaction chain. The only previous study, to our knowledge, to consider the effects of grazing for host-parasitoid interactions was carried out in anthropogenic grassland (Kruess & Tscharntke 2002b). The present study considers the importance to a host-parasitoid interaction of habitat heterogeneity arising from anthropogenic disturbance of semi-natural woodland.

We hypothesised, firstly, that cattle act as ecosystem engineers in birch woodland fragments with indirect, cascading and direct effects on the host-parasitoid interaction. Indirect, cascading effects on host insect and parasitoid populations would arise as a result of cattle grazing and trampling reducing plant competitive exclusion, creating niche space and thus increasing the density and evenness in the thistle distribution. We predicted that: i) the presence of cattle would increase the density, and create a more even dispersion, of thistles compared to ungrazed woodlands; ii) parasitoid density would be positively correlated to host insect density at the individual host plant and habitat scale; and iii) an increase in host insect and parasitoid densities, and the amount of parasitism, will result from the greater density and more even dispersion of host-plants in grazed woods. We also predicted that cattle would modify the woodland habitat producing a more diverse, compositionally and structurally different plant assemblage compared to the ungrazed woodlands. This grazing-dependent habitat heterogeneity would directly affect the abundance of the two species of seed herbivores, their shared parasitoid and the amount of parasitism.

Secondly, we hypothesised that grazing-independent host-plant heterogeneity (stature, architecture and proportion of open inflorescences) would affect the density of both host insect and parasitoid populations with the prediction that taller, bushier plants with more flowers will support greater densities of herbivores and parasitoids, and increased parasitism.

6.2 Methods

6.2.1 Tri-trophic system

The marsh thistle *Cirsium palustre* L. is a multi–stemmed biennial ranging from 50 to 120cm in height with composite flowerheads clustered at the end of each stem. *Cirsium palustre* tends to have an aggregated dispersion where it occurs naturally (Williams *et al.* 2001). Flowering occurs from early June to mid–September and seed herbivores attack the flowerheads - the most common of which are tephritid flies (Diptera: Tephritidae). The adult tephritid fly inserts its eggs among the florets of recently opened flowerheads and the larva burrows into the flowerhead where it feeds on the receptacle and seeds (Janzon 1984; Jones *et al.* 1996). Two tephritid species were considered. *Tephritis conura* Loew is univoltine with gregarious larvae (up to seven conspecific larvae per capitulum) feeding during June and July, and the adult emerging in August to over-winter (Janzon 1984; White 1988; Romstöck-Völkl 1990a). *Xyphosia miliaria* Schrank, on the other hand, is generally solitary (occasionally two conspecific larvae per capitulum) and bivoltine: the first generation completes larval development and emerges as an adult between July and September, the second completes larval feeding by the autumn overwintering in the final instar to pupate in spring, and emerge as the adult fly between May and July (White 1988). In Britain, *T. conura* has also been recorded feeding on *Cirsium heterophyllum* (L.) Hill (White 1988), a species not seen in the sites studied here. The alternative host plant of *X. miliaria*, which occurred in some of the grazed study sites, is *Cirsium arvense (L.)* (White 1988). The tephritids share a parasitoid *Pteromalus (syn: Habrocytus) elevatus* (Walker) (Hymenoptera: Pteromalidae). This endoparasitoid probes the thistle capitula with its ovipositor and deposits eggs externally on the tephritid larvae (Hoebeke & Wheeler 1996). The peak in parasitoid oviposition occurs during early to mid–August (Jones *et al.* 1996). The parasitoid overwinters within the larval host (yielded from *X. miliaria* and late season *T. conura*) or possibly as an adult (when yielded from early season *T. conura*) (A.J.Vanbergen. pers.obs).

Plate 6.1. *Pteromalus elevatus*

Plate 6.2. *Xyphosia miliaria*, one of the two tephritid species studied here

6.2.2 Sites and experimental design

20 birch (*Betula pendula / pubescens*) woodland sites were selected in the Deeside region of Aberdeenshire (57°3.0′N, 2°30.2′E - 57°3.3′N, 2°57.9′E) according to whether they supported existing populations of *C. palustre* and to the presence (n = 10) or absence (n = 10) of livestock grazing. Care was taken to ensure that sites selected were not geographically confounded (Figure 5-1). Livestock in the grazed sites were predominantly cattle (n = 10), with occasional and additional grazing by sheep (n = 3) and horses (n = 1), and this management had been in place for at least the preceding 10 years. The low incidence of grazing by wild ungulates (i.e. roe deer) was not measured because it was assumed to be of minimal importance when compared with the intensive livestock management. No other systematic management (e.g. logging) occurred at either grazed or ungrazed sites. At the end of April (coincident with the date of birch budburst) eight second-year *C. palustre* thistles were transplanted, from two nearby sites, into each of the woodland locations. Within each site replicate plants were randomly assigned to a position within a 4 x 4 grid (15m^2) with each point on that grid separated by 5m. The centre of the grid was situated at least 50m from the woodland edge and, at most, 50m from the pre-existing population of thistles. Prior to flowering cattle trampling destroyed some replicate thistles (18 %) and neighbouring thistles of local origin acted as replacements. No evidence of vertebrate grazing was seen on experimental thistles during the course of the experiment.

6.2.3 Insect abundance

Colonisation of the thistles by both the tephritid herbivores (*X. miliaria* and *T. conura*) and their shared parasitoid (*P. elevatus*) was assessed by bagging and excising the thistle stem (14 - 15 August 2003). 12 seed heads were randomly selected from each bagged thistle (160), a total of 2,112 flowerheads, and dissected for tephritid pre-pupae or pupae. These were removed and placed in labelled Eppendorf™ tubes to rear-on the adult tephritid or parasitoid within the host. Identification of *X. miliaria* and *T. conura* was based on White (1988) and *P. elevatus* on (Hoebeke & Wheeler 1996).

6.2.4 Habitat variables

Six $1m^2$ quadrats per site were randomly placed on points on the aforementioned grid not occupied by experimental thistle replicates, and an assessment was made in each quadrat of a range of field layer variables (28 July - 12 August 2003). The species richness of functional groups (forbs, grasses) and total vascular plant richness was determined, and the percentage cover for each vascular plant species and functional group (forbs, grasses, bryophyte) visually estimated. The proportion of bare, disturbed soil surface arising from cattle trampling was also recorded in each quadrat. The percentage cover of the tree canopy above each quadrat was estimated using a canopy densiometer (Forestry Suppliers Inc. USA) and at the four corners of each quadrat the maximum sward height (mm) was recorded. The area of each birch woodland fragment was determined from digitised maps (Ordnance Survey, UK) using GIS (ArcGIS) (Figure 5-1).

6.2.5 Host plant variables

Towards the end of the adult tephritid activity period (20 – 25 July 2003) a number of host-plant level parameters were measured to quantify the effect of heterogeneity between individual plants on insect abundance and parasitism rates. The structure of each thistle replicate was quantified by measuring: the height (cm) of the stem (or tallest stem in case of multi-stemmed individuals), the architectural complexity (number of stems plus branches) and the proportion of open inflorescences. The degree to which the density and distribution of the pre-existing *C. palustre* populations in each birch wood affecting colonisation of experimental thistles was assessed. *C. palustre* density was mapped in a $100m^2$ quadrat centred on the experimental grid. The quadrat was sub-divided into $5m^2$ cells, giving a total of 400 cells per $100m^2$, and the number of pre-existing thistles in each cell was recorded. The density and aggregation ($s / \bar{x}$) (Hassell *et al.* 1991) of *C. palustre* host-plants was derived at two spatial scales ($100m^2$, $25m^2$) around the experimental thistles, set by what is known about tephritid and pteromalid maximum dispersal distance (Jones *et al.* 1996), and these data were used in subsequent tests.

6.2.6 Statistical analysis

6.2.6.1 Effect of grazing on the habitat and plant assemblage

Whether mean habitat variables between the grazed and ungrazed sites were significantly different was determined with Wilcoxon signed-rank tests. Plant assemblage structure was assessed using redundancy analysis (RDA; CANOCO version 4.5); a constrained form of principal components analysis (PCA) that identifies trends in the scatter of species data that are linearly related to a set of constraining, explanatory variables (ter Braak & Šmilauer 1988; Jongman, ter Braak & van Tongren 1995). Vascular plant species with <10 % cover (constituting only 1% of the total vegetation) when summed across all sampled sites were removed from the data set to avoid the RDA being biased by species that occurred only in a limited number of sites; data were log transformed prior to analysis (ter Braak & Šmilauer 1988; Jongman *et al.* 1995). RDA was used to relate the percentage cover of vascular plant species to measured explanatory variables (canopy density, sward height, proportion of bare and trampled soil, bryophyte and leaf-litter cover). Variables derived from the plant species data (forb and grass percentage cover, vascular plant species richness) were fitted as supplementary variables only in order to illustrate further trends in the plant assemblage and do not affect the variance explained by the RDA of the vascular plant assemblage. The significance of the explanatory variables in structuring the plant assemblage was determined with a forward selection procedure using Monte-Carlo tests constrained within sites (9999 permutations). Thus the model presented is a partial redundancy analysis (pRDA) controlling for site-level variance when assessing the impact of grazing-dependent habitat variation on the plant assemblage.

6.2.6.2 Effect of grazing on thistles, herbivore and parasitoid populations

Data were analysed using generalised linear mixed models (GLMM) (SAS version 8.01, SAS Institute) at two scales: i) the site (n=20) to test for treatment (grazed or ungrazed) and cattle-dependent habitat effects, and ii) individual plants (n=160) nested within site to test for host-plant effects. Dependent variables were host-plant (*C. palustre*) density and aggregation ($s / \bar{x}$), counts per plant and mean counts per site of tephritid (*X. miliaria* and *T. conura*) and parasitoid (*P. elevatus*) populations. Parasitism was modelled with the count of *P. elevatus* as the dependent variable offset against the log transformed count of host insect pupae. Poisson error distributions were fitted to all count data except mean parasitoid counts as these data had residuals that were normally distributed. Solution of fixed explanatory (treatment, habitat and host-plant variables, host insect density) and random (categories: 'site' and 'thistle nested within site') effects was estimated by residual maximum likelihood (REML) (Schall 1991; Elston *et al.* 2001). Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell *et al.* 1996). Details of the models run to test our hypotheses are summarised in Table 6-1. Model simplification was by step-wise elimination of the least significant term until the most parsimonious model was found and F-ratios of fixed effects using adjusted sums of squares (Type 3 tests) are reported. To assess the effect of cattle-dependent habitat heterogeneity on the abundance of tephritids and parasitoid, and percent parasitism the term 'treatment' was replaced with specific habitat variation (e.g. plant species richness) between grazed and ungrazed sites. Owing to inter-correlation between habitat variables (Table 6-2) the separation of their effects by step-wise multivariate regression was confounded. We therefore performed PCA on these habitat data. The orthogonal PCA axes derived (which are uncorrelated with each other, but principally correlated with specific habitat variables) were then used as the fixed effects in the models. This was done to separate the effect of these inter-correlated habitat variables on the insect abundance and reduce the number of explanatory variables in an ecologically meaningful manner. Similarly variables describing heterogeneity between host-plants were inter-correlated (Table 6-2) and we treated these in the same way.

Table 6-1. Structure of GLMM models run to test the effect of treatment (cattle presence or absence), grazing-dependent heterogeneity, host-plant heterogeneity, host-insect density on host-plant, tephritid seed herbivore, parasitoid abundance and the amount of parasitism in birch woodlands.

Test	Dependent	Scale	Independent
Effect of grazing on host-plant			
	Host-plant density	Habitat (25 & 100m^2)	Treatment
	Host-plant aggregation	Habitat (25 & 100m^2)	Treatment
Effect of host-plant distribution on insects			
	Host-insect count	Habitat (25 & 100m^2)	Treatment, Host-plant density or aggregation
	Parasitoid count	Habitat (25 & 100m^2)	Treatment, Host-plant density or aggregation
	Parasitism	Habitat (25 & 100m^2)	Treatment, Host-plant density or aggregation
Effect of cattle presence on insect density			
	Host-insect count	Habitat	Treatment
	Parasitoid count	Habitat	Host insect count, Treatment
	Parasitism	Habitat	Treatment
Host-parasitoid correlation			
	Mean parasitoid count	Habitat	Mean host insect count, Treatment x Mean host-insect count
	Parasitoid count	Host-plant	Host-insect count
Effect of cattle-dependent habitat heterogeneity			
	Host-insect count	Habitat	PCA1, PCA2
	Parasitoid count	Habitat	Host-insect count PCA1, PCA2
	Parasitism	Habitat	PCA1, PCA2
Effect of host-plant heterogeneity			
	Host-insect count	Host-plant	PCA1, PCA2
	Parasitoid count	Host-plant	Host-insect count PCA1, PCA2
	Parasitism	Host-plant	PCA1, PCA2

Table 6-2. Inter-correlation between birch habitat and host-plant variables. Values are Pearson's correlation coefficients (SAS version 8.01) P<0.05*, P<0.01**, P<0.001***. Habitat variables are the percentage cover of bare soil, forbs, grasses and bryophytes, tree canopy density (%), height (mm) of the vegetation (Sward), and the number of vascular plant species (Plant *S*), forb species (Forb *S*) and grass species (Grass *S*). Host-plant variables are: architecture - the total number of stems and branches per plant, height - the height (cm) of the tallest stem of each plant, and inflorescence - the proportion of flowers open by the end of the adult tephritid activity period.

Habitat	Sward	Plant *S*	Forb *S*	Grass *S*	Bare soil	Forb	Grass	Bryophyte
Canopy	0.05	-0.59***	-0.41***	-0.50***	-0.18*	-0.20**	-0.13	0.44***
Sward		-0.36***	-0.54***	0.16	-0.48***	-0.49***	0.31***	-0.10
Plant *S*			0.86***	0.56***	0.47***	0.43***	-0.20**	-0.33***
Forb *S*				0.27**	0.52***	0.69***	-0.30***	-0.39***
Grass *S*					0.27**	0.13	0.42***	-0.52***
Bare soil						0.47***	-0.09	-0.38***
Forb							-0.16*	-0.44***
Grass								-0.57***
Host-plant	Arch.	Height						
Inflorescence	0.29**	0.31***						
Architecture		0.49***						

6.3 Results

6.3.1 Effect of cattle on the plant assemblage and host-plant

The presence of cattle in birch woodlands altered the plant assemblage in this habitat. The grazed sites had a greater species richness of vascular plants, and forbs in particular, compared to ungrazed locations (Table 6-3). The percentage cover of bryophytes (principally *Hylocomium splendens* (Hedw.) Br. Eur.– an undercanopy species) was significantly decreased in the grazed locations with a concomitant increase in the overall percentage cover of forbs (particularly genera such as *Ranunculus* L. and *Trifolium* L.) (Figure 5-4, Table 6-3). In addition, grazed sites had a less dense tree canopy, a greater proportion of bare earth on the soil surface (a consequence of trampling by cattle) and a lower mean sward height compared to the ungrazed situation (Figure 5-4, Table 6-3).

Plant assemblage structure was affected by the presence of grazing livestock; pRDA revealed a clear separation between plant assemblages depending on whether they were grazed or not (Figure 5-4). The axes of the pRDA were significant (Monte-Carlo global permutation tests: first canonical axis: $P = 0.008$, all canonical axes: $P = 0.0006$) and it was the first axis of the pRDA that explained most of the variation (eigenvalue = 0.08) in the plant species assemblage (Figure 5-4). This primary axis of variation was positively correlated with increasing bryophyte percentage cover (correlation coefficient = 0.74), tree canopy density (0.56), plant litter cover (0.56) and average sward height (0.50), and negatively correlated with the amount of disturbed and trampled soil (-0.56). These fitted environmental variables explained 14% of the total variance in the plant species percentage-cover data. Plant assemblages in grazed sites were positively related to greater amounts of soil disturbance (Monte-Carlo $P = 0.04$, Figure 5-4) and negatively associated with lower levels of bryophyte cover ($P = 0.004$, Figure 5-4), tree density ($P = 0.003$, Figure 5-4), sward height ($P = 0.04$, Figure 5-4) and reduced amounts of plant litter on the soil surface ($P = 0.02$, Figure 5-4). Grazed plant assemblages were characterised by high species diversity and forb percentage cover (Figure 5-4). There was no statistical support for the prediction that the density or dispersion of thistles was affected by the presence of cattle at any of the spatial scales examined (Table 6-4).

Table 6-3. Wilcoxon signed-ranks comparison of mean habitat variables from grazed (n =10) and ungrazed (n =10) sites.

Variable	Mean		SD		z	P
	Grazed	Ungrazed	Grazed	Ungrazed		
Plant species richness	26.3	16.8	6.3	5.1	2.88	0.002
Grass species richness	7.4	6.0	1.8	1.9	1.34	0.09
Forb species richness	15.5	6.4	4.1	3.9	3.41	0.0003
Bare ground (%)	18.0	1.2	0.1	0.0	2.82	0.002
Sward height (mm)	347.1	503.8	161.7	176.1	-1.85	0.03
Grasses (%)	76.9	76.0	14.1	30.7	-0.57	0.285
Forbs (%)	42.6	13.7	20.1	8.6	3.21	0.0007
Bryophytes (%)	7.3	26.0	7.3	6.6	-2.83	0.002
Canopy density (%)	63.0	87.4	0.3	0.1	-1.70	0.04

Table 6-4. The effect of treatment (grazed or ungrazed woodland) on the density and aggregation of *C. palustre* host-plants at two spatial scales (100m^2, 25m^2) centred on the experimental grid and effect of host-plant density and aggregation on the abundance of two seed herbivores (*X. miliaria, T. conura*) their parasitoid *P. elevatus* and the proportion of parasitized *T. conura*. F-ratios and *P*- values are from GLMM with Poisson errors and log link, † P = 0.05 ** P < 0.01.

Thistle	**Grazed**	**Ungrazed**	**Treatment**	***X. miliaria***	***T. conura***	***P. elevatus***	**Parasitism**
25 m^2	Mean (SD)		F (d.f.)	F (d.f.)	F (d.f.)	F (d.f.)	F (d.f.)
Density	4.90 (5.28)	3.60 (5.99)	0.01 (1,14)	3.94 (1,18)	0.25 (1,14)	0.00 (1,13)	0.87 (1,10)
Aggregation	1.28 (1.16)	2.19 (1.71)	0.55 (1,13)	1.25 (1,11)	2.47 (1,15)	**10.82 (1,18)****	**9.98 (1,18)****
100 m^2							
Density	58.0 (34.8)	73.8 (85.6)	0.16 (1,17)	3.89 (1,11)	0.02 (1,15)	0.00 (1,15)	0.92 (1,15)
Aggregation	3.82 (2.23)	5.03 (3.16)	0.55 (1,16)	2.80 (1,17)	1.57 (1,17)	**4.50 (1,13)†**	3.48 (1,16)

6.3.2 Effect of cattle presence on tephritid and parasitoid populations

The two tephritid species dominated the endophagous capitulum fauna; only rarely were microlepidopteran and hymenopteran (*Palloptera* spp.) larvae found in samples. The response of the tephritid herbivores to the presence of cattle in birch woodlands contrasted strongly: *Xyphosia miliaria* was not affected by the presence of grazing livestock (Table 6-5, Figure 6-1a) while *Tephritis conura* increased in number in grazed compared to ungrazed birch woodlands (Table 6-5, Figure 6-1a). Parasitoid abundance was also significantly affected by cattle presence with greater numbers found in grazed woodlands compared with the ungrazed situation (Table 6-5, Figure 6-1a). Furthermore, the percentage of *T. conura* pupae parasitised was significantly higher in grazed woodlands compared with ungrazed woodlands (Figure 6-1b, $F_{1, 18} = 9.69$, $P = 0.006$), suggesting this increase in parasitism could not be solely explained by increasing host insect abundance.

6.3.3 Tephritid-parasitoid interactions

There was a strong, positive association between *T. conura* and parasitoid number at the scale of host-plant (Figure 6-2a, $F_{1, 118} = 82.73$, $P < 0.0001$) and woodland site (Figure 6-2b, $F_{1, 18} = 69.87$, $P < 0.0001$). Parasitoid abundance was significantly affected by the interaction between host insect number (*T. conura*) and cattle presence or absence at the woodland site scale (*T. conura* x treatment: $F_{1, 18} = 9.91$ $P = 0.006$) with parasitism of *T. conura* at grazed sites occurring at more than twice the rate found in ungrazed sites (Figure 6-2b). Parasitoid abundance was not correlated with *X. miliaria* abundance either at the host-plant ($F_{1, 158} = 0.82$, NS) or woodland site ($F_{1, 18} = 0.03$, NS) scales. There was no correlation between the abundance of the tephritid herbivores at the host plant scale ($F_{1, 158} = 1.83$, NS) or at the scale of the woodland site ($F_{1, 18} = 0.49$, NS).

Table 6-5. The effect of grazing, cattle-driven environmental and host-plant heterogenity on the abundance (counts) of two tephritid herbivores *Xyphosia miliaria*, *Tephritis conura* and their parasitoid *Pteromalus elevatus*. Summary of GLMM models (SAS version 8.02) with Poisson error structure and log link function, F-ratios of significant fixed effects adjusted to account for other significant variables, non-significant terms were eliminated in step-wise manner. Due to inter-correlation between habitat and host plant variables PCA axes scores of covariates were obtained and used as explanatory terms in the model. Principal components correlated with the orthogonal axes scores are given in parentheses (+ vascSR - plant species richness, + forbSR – forb species richness, +forb – % cover of forbs, + Arch – Host-plant architecture (number of branches and stems per thistle), +Flower - % of open inflorescences during the adult flight period, +Height – height (cm) of the thistle flower stalk).

Fixed effect	***X. miliaria***					***T. conura***					***P. elevatus***				
	intercept	estimate	*df*	F	*P*	intercept	estimate	*df*	F	*P*	intercept	estimate	*df*	F	*P*
Treatment (Grazed or Ungrazed)	-0.89	-0.21	1,14	0.11	0.74	-1.64	1.61	1,17	7.75	0.012	-2.98	1.97	1,18	12.37	0.003
Habitat															
T.conura density											-2.72	0.24	1,37	49.15	<.0001
PCA1 (+vascSR, +forbSR, +forb)	-1.03	0.01	1,13	0.00	0.97	-0.85	0.45	1,17	9.18	0.007		0.38	1,15	6.60	0.02
PCA2 (+grassSR, +grass,+sward)		0.23	1,16	0.92	0.35		0.16	1, 24	0.49	0.49		0.01	1,19	0.00	0.97
Host plant															
T.conura density											-2.89	0.21	1,31	39.19	<.0001
PCA1 (+Arch, +Height)	-0.96	-0.16	1,131	2.18	0.14	-0.88	0.44	1,144	6.68	0.01		0.79	1,138	10.59	0.001
PCA2 (+Flower)		0.02	1,141	0.01	0.92		0.80	1,138	10.25	0.002		0.84	1,80	5.30	0.024

Figure 6-1. The effect of the presence of cattle grazing on (a) the abundance of two tephritid herbivores (*Tephritis conura* $F_{1,17} = 7.75$ $P = 0.012$ and *Xyphosia miliaria* $F_{1,14} = 0.11$, NS) and their shared parasitoid (*Pteromalus elevatus* $F_{1,21} = 8.55$, $P = 0.008$), and (b) the proportion of parasitized *T. conura* ($F_{1,20} = 8.98$, $P = 0.007$). Mean values ± SE derived from 10 grazed and 10 ungrazed birch woodland sites.

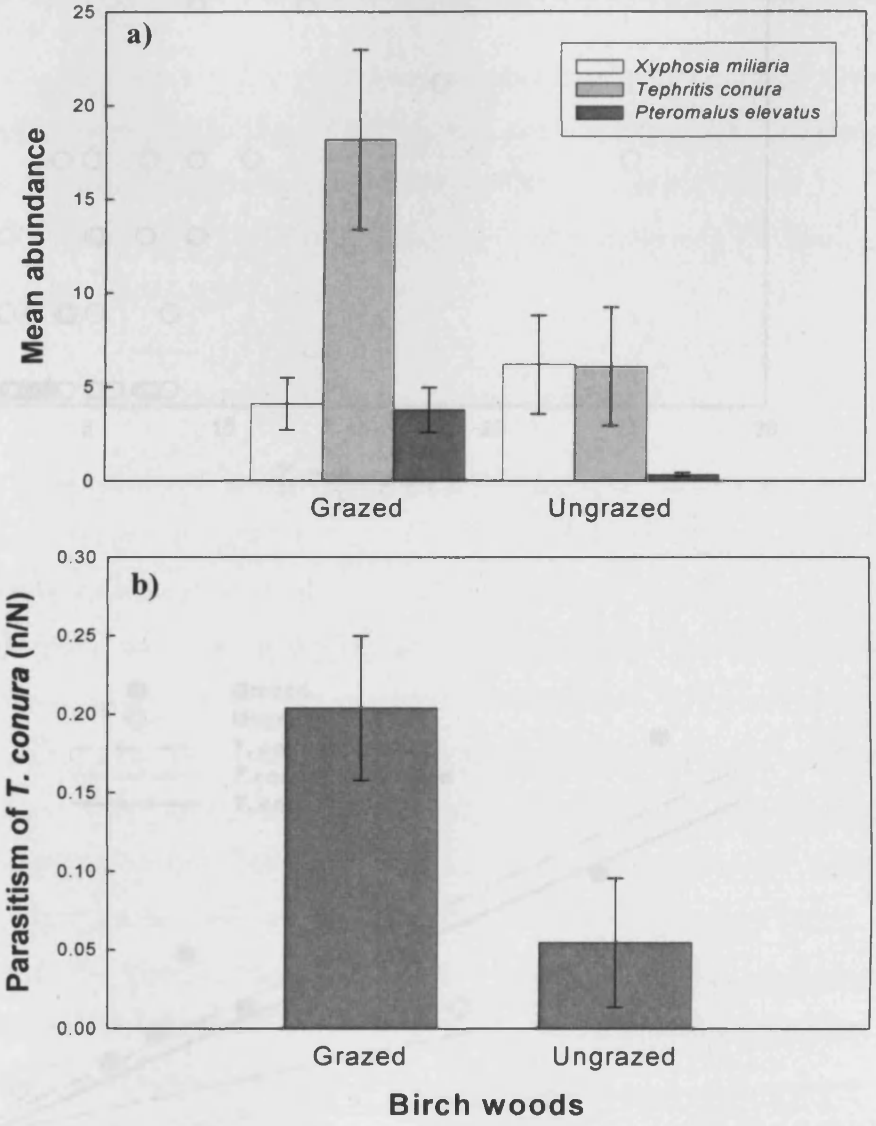
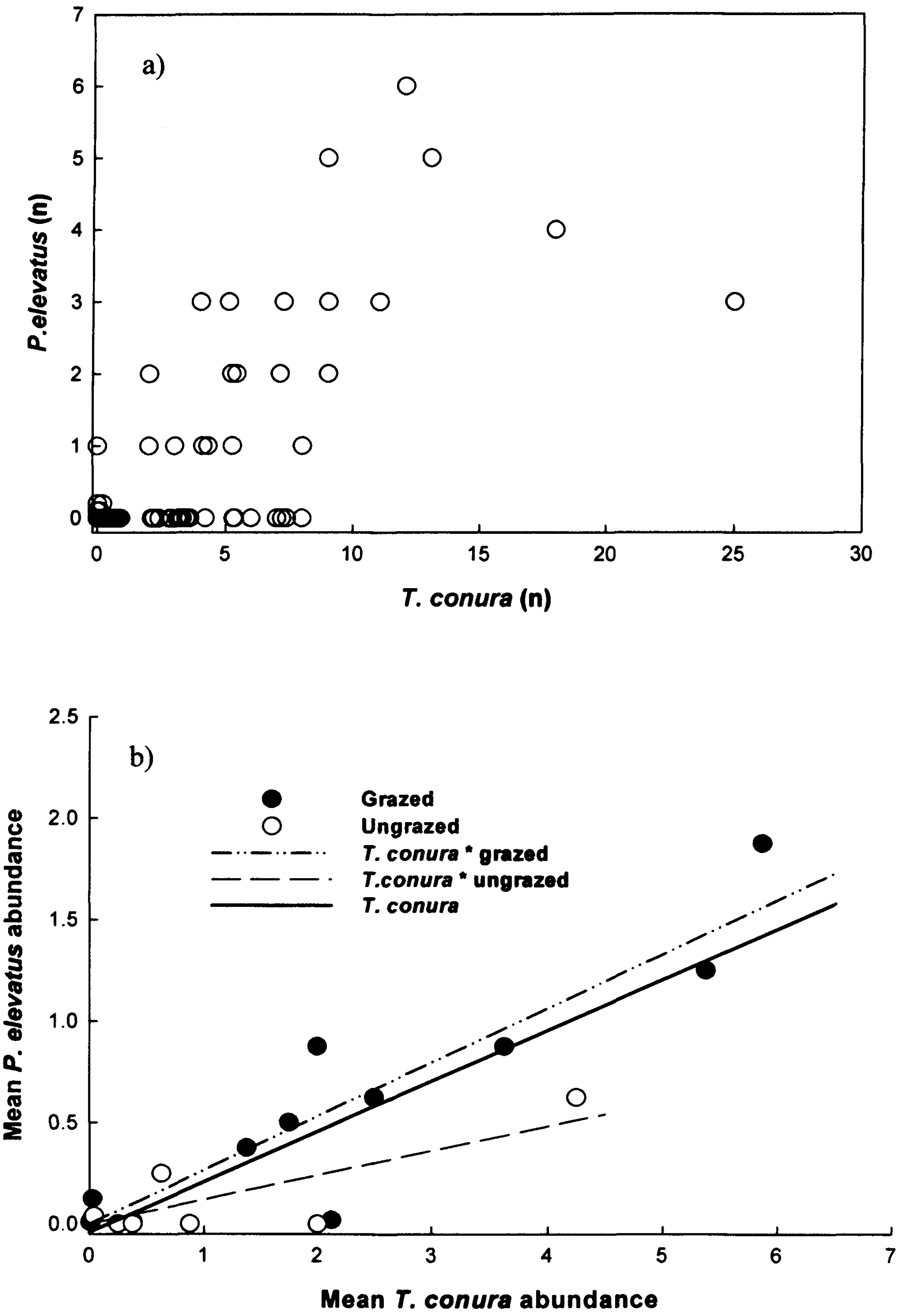


Figure 6-2 Relationship between the abundance of the parasitoid *P. elevatus* and its host *T. conura* at the scale of (a) the individual host plant ($F_{1,118} = 82.73$, $P < 0.0001$), and (b) the woodland site (*T. conura* $F_{1,18} = 69.87$, $P < 0.0001$, *T. conura* x treatment $F_{1,18} = 9.91$ $P = 0.006$). Fitted lines from GLM with normally distributed error distribution.



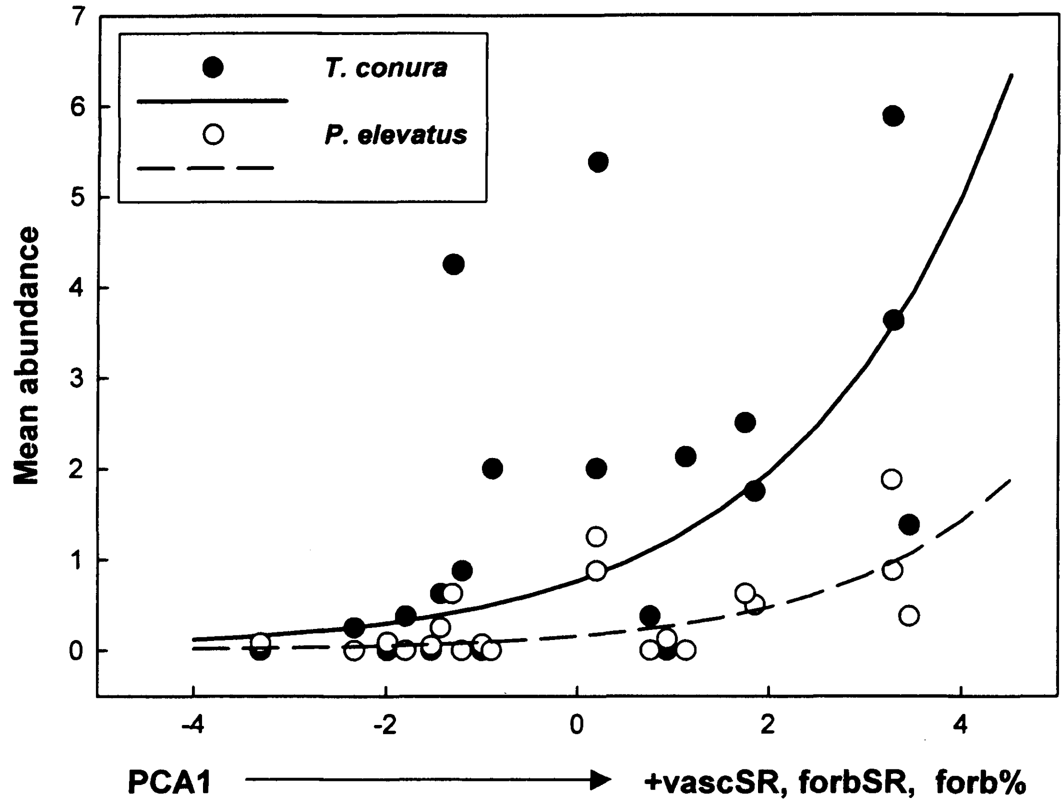
6.3.4 Cattle habitat engineering effect on tephritid populations

The compositional changes to the plant assemblage driven by cattle grazing directly affected the *T. conura* population. When *T. conura* abundance was modelled against the orthogonal PCA axes of the habitat variables it was the first ordination axis - positively correlated with forb species richness (eigenvector = 0.46), plant species richness (eigenvector = 0.45) and forb cover (eigenvector = 0.38) - that was significantly and positively correlated with the numbers of this herbivore (Table 6-5, Figure 6-3). The second PCA axis - correlated with the percent cover (eigenvector = 0.56) and species richness of grasses (eigenvector = 0.43) and average sward height (eigenvector = 0.43) – did not correlate with *T. conura* density. *X. miliaria* was not significantly affected by either of the PCA axes (Table 6-5). The woodland area had no significant effect on the abundance of either herbivore (*T. conura* $F_{1,17} = 0.26$, NS, *X. miliaria* $F_{1,12} = 3.50$, NS).

6.3.5 Cattle habitat engineering effect on the parasitoid population

Grazing-dependent changes to the composition of the plant assemblage both directly and indirectly (via changes in host insect density) affected the highest trophic level. The abundance of the parasitoid, *P. elevatus*, was positively and significantly correlated with the first PCA axis (positively correlated with vascular plant species richness, forb species richness and percent cover) (Figure 6-3). This is partially explained by the observed increase in floral richness cascading up to the parasitoid population via changes to host-insect density (Table 6-5, Figure 6-2b). There remained, however, after accounting for host density, a direct and positive effect of this grazing-dependent habitat variation on parasitoid abundance (Table 6-5, Figure 6-3). Furthermore percent parasitism (proportion of *T. conura* pupae parasitised) in these woodlands was also positively related ($F_{1,17} = 6.85$, $P = 0.02$) to this grazing-dependent habitat variation represented by the first axis of the PCA. The woodland area had no significant effect on parasitoid abundance ($F_{1,17} = 0.09$, NS).

Figure 6-3 Relationship of *T. conura* and *P. elevatus* abundance to the first principal component of grazing-dependent habitat heterogeneity (correlated with plant (vascSR) and forb (forbSR) species richness and forb percentage cover (forb%)). *T. conura* $F_{1,17} = 9.18$, $P = 0.007$; *P. elevatus* $F_{1,15} = 6.60$, $P = 0.02$. Fitted line derived from GLMM with Poisson error structure and log link function.



6.3.6 Host-plant level effects on tephritid and parasitoid populations

Plant structural variables, namely the height of the stem, architecture (number of branches and stalks per thistle) and the proportion of open inflorescences per thistle were significantly inter-correlated (Table 6-2). None were significantly affected by the presence of cattle (architecture $F_{1,18} = 0.14$ NS, height $F_{1,18} = 0.46$ NS, inflorescences $F_{1,18} = 0.17$ NS). Both the first (correlated with plant architecture - eigenvector =0.61, and stem height - eigenvector =0.62) and second (correlated to the proportion of open inflorescences - eigenvector = 0.86) PCA axes were significantly and positively related of the abundance of *T. conura* and *P. elevatus* (Table 6-5). Taller, bushier thistles with a larger proportion of open flowers supported greater numbers of *T. conura* and, after controlling for variance due to host tephritid density, the parasitoid (Table 6-5). Percent parasitism was positively correlated with the first ($F_{1,67} = 12.08$, $P = 0.0009$) and the second PCA axes ($F_{1,49} = 5.72$, $P = 0.02$). There was no significant effect of host-plant structure on *X. miliaria* abundance (Table 6-5). Furthermore, independent of grazing, neither tephritid herbivore was affected by the density or degree of aggregation of their host plants at any spatial scale measured (Table 6-4). Parasitoid density, however, showed a highly significant, negative relationship with the aggregation of thistles. Parasitoids occurred in greater numbers where the thistle distribution was more clumped at 25m^2 and marginally at the 100m^2 scale (Table 6-4). The level of parasitism also increased where thistles had a more clumped distribution at the smallest spatial scale measured (Table 6-4).

6.4 Discussion

6.4.1 Cascading and direct effects of cattle on a tri-trophic system

There was no effect of cattle engineering on the density or dispersion of thistles, and therefore no grazing-driven cascade via the host-plant to the abundance of the higher trophic levels or the amount of parasitism in the tri-trophic system. The presence of cattle did, however, have consequences for one of the two host-parasitoid interactions studied. An increase was seen in the abundance of the herbivore, *T. conura*, and its parasitoid in the grazed compared to the ungrazed situation. No change was observed in the abundance of the second herbivore, *X. miliaria*; the reason for the lack of a response remains unclear. This provides partial support for our prediction that the effects of cattle grazing would influence primary consumers. While cattle grazing did not initiate a bottom-up cascade from host-plant to herbivore, grazing did lead to an increase in *T. conura* abundance that did cascade up to the tertiary trophic level of the interaction chain. The number of *T. conura* was highly correlated with the increase in parasitoid abundance in grazed woodland and the presence of cattle doubled the parasitism rate contributing to the higher levels of parasitism in grazed sites.

Despite not affecting the tephritids' host-plant, cattle did act as ecosystem engineers (Jones *et al.* 1997) facilitating (via grazing and trampling) compositional (e.g. increased plant species richness) and structural (e.g. decrease in tree density) changes to the wider plant assemblage (Hobbs 1996). The grazed woodlands had a more diverse field layer and supported a plant assemblage compositionally different to that in ungrazed woods. In ungrazed sites the plant assemblage was dominated by competitively superior plant species (e.g. *Molinia caerula* L. (Moench), *Pteridium aquilinum* (L.) Kuhn, *Holcus* L. *spp.*). Grazing reduced the cover of these competitive-dominants (Grant *et al.* 1996; Humphrey & Swaine 1997; Pakeman 2004) and facilitated a structurally simpler but compositionally diverse sward including grazing tolerant species (e.g. *Ranunculus repens* L., *Trifolium repens* L., *Poa trivialis* L.) more typical of open, grassland.

Changes in plant assemblage structure driven by cattle appear responsible for the observed changes in abundance of the higher trophic levels of the interaction chain. The abundance of *T. conura, P. elevatus* and percent parasitism were positively correlated with the first principal component of the habitat variables (increased plant and forb species richness, and forb cover). This suggests that the greater floral diversity of the grazed sward may provide nectar resources throughout the flight period leading to, for example, improved fecundity, longevity and survival (Jervis *et al.* 1993; Romstöck-Völkl 1990a; Jervis 1998; Heimpel & Jervis 2005). Cattle, therefore, affected the host insect in an indirect manner, not mediated by the host-plant but by wider plant diversity, and this effect cascaded up to the highest trophic level, the parasitoid population. In addition to this trophic cascade there was evidence of a further, direct effect of habitat engineering by cattle on the parasitoid populations: after controlling for host insect density there remained a positive correlation between the increased floral richness in grazed woods, parasitoid number and percent parasitism. In contrast to studies that have demonstrated specific host-plant effects on parasitoids (Englishloeb *et al.* 1993; Van Nouhuys & Hanski 1999) this study revealed that parasitism rates occurring within a host-plant were in part dependent on the wider plant community diversity. This is analogous to studies that have found at coarser spatial scales the amount of parasitism occurring in a habitat patch is influenced by the composition or heterogeneity of the surrounding landscape (Kruess 2003; Thies *et al.* 2003). Parasitism is therefore sensitive to environmental heterogeneity from sources beyond the immediate host or habitat patch highlighting the potential for trophic interactions to be altered by anthropogenic disturbance.

The role of grazing in influencing host-parasitoid interactions had, as far as we are aware, previously been considered only in one other study which demonstrated a decline in parasitoid number and parasitism rates associated with intense grazing (Kruess & Tscharntke 2002b). In contrast, we showed a positive consequence of grazing (and the environmental heterogeneity produced) for parasitoid abundance and parasitism rates. This distinction may have arisen as a result of differences between the study systems. Kruess & Tscharntke (2002b) considered how intense grazing in an anthropogenic grassland habitat reduced the height of the vegetation and led to a decline in the numbers of insect hosts and their parasitoids. In this case, the introduction of cattle to birch woodlands is a perturbation of a semi-natural habitat, leading to a shift in the plant assemblage structure towards one more typical of open grassland. A consequence of this habitat modification was an increase in floral resources with unforeseen, positive consequences (direct and indirect) for parasitoid density and parasitism rates.

6.4.2 Direct and indirect host-plant effects on higher trophic levels

Given the intimate relation (reproduction and larval feeding) between both these seed herbivores and their host plant, heterogeneity in host plant attractiveness or larval resources would be expected to affect strongly on the probability of colonisation by the herbivores (Romstöck-Völkl 1990a; Williams *et al.* 2001). *T. conura* density was determined by the number of inflorescences and overall plant size, either because the larger individual plant with many inflorescences is more apparent in the habitat (Prokopy 1968; Aluja & Prokopy 1993) or because it offers more resources in terms of mating, oviposition, and larval growth and survival (Romstöck-Völkl 1990a; Williams *et al.* 2001). Parasitoid population density and parasitism rate was also greater on larger plants with many inflorescences, partly explained by the correlation between host (*T. conura*) density and these host-plant parameters, but also by a direct influence of this plant level heterogeneity on the parasitoid. The failure to detect any relationship between *X. miliaria* and the various host plant structural variables is unexpected, particularly given the low occurrence in grazed and absence in ungrazed sites of the alternative congeneric host (*C. arvense*). One possibility is that the variables measured here are not those employed by *X. miliaria* for locating and colonising hosts.

In direct contrast to previous studies (Jones *et al.* 1996; Williams *et al.* 2001) there was no effect of the number or aggregation of the pre-existing thistle population on the abundance of either tephritid species. It may be that the lack of a response to host plant density or aggregation reflects the overall commonness of the plants in both grazed and ungrazed birch woods. There may be little selective pressure for these insects, despite gradients in thistle distribution within and between sites, to distribute themselves non-randomly as the source of their food is abundant overall (Jakobsen & Jjohnsen 1987). In contrast, parasitoid density and percent parasitism of *T. conura* increased in areas where thistles were aggregated. It appears likely, therefore, that the parasitoid uses the thistles as an environmental signal to initiate searching for the host insect and may find it simpler to locate host-plant patches rather than the more cryptic host insect (Cappuccino 1992). The difference between the response of the herbivore *T.conura* and the parasitoid to thistle aggregation may be explained as one strategy by the herbivore to avoid its enemy: in ovipositing randomly the herbivore may spread the risk of parasitism by decoupling the larval distribution from the host plant distribution in a predictable manner (Cappuccino 1992; Williams *et al.* 2001).

6.5 Conclusions

Grazing-dependent habitat heterogeneity and grazing-independent host-plant heterogeneity influence the studied host-parasitoid interactions in both a direct and indirect, cascading manner. Grazing cattle in forests can erode the strength and extent of mutualistic (Vazquez & Simberloff 2003) and antagonistic insect interactions (Kruess & Tscharntke 2002); however in this study grazing cattle more than doubled the rate of parasitism compared with the ungrazed scenario. This provides a rare example of a tertiary trophic level being positively rather than negatively affected by anthropogenic disturbance (Didham *et al.* 1998; Davies *et al.* 2000; Kruess & Tscharntke 2002). This was not a conventional bottom-up cascade because grazing did not alter the density, dispersion or architecture of the host-plants underpinning this host-parasitoid interaction. Instead it was grazing-driven changes to the diversity of the wider plant assemblage, cascading up via the insect host and acting directly on the parasitoid populations, which led to the observed increase in parasitism. Host-plant heterogeneity also affected parasitoid density and percent parasitism both indirectly (via host insect density) and directly. Along with scale (habitat and host-plant) and the relative role of vertical effects (bottom-up versus top-down) the importance of wider environmental heterogeneity, and not only those features intrinsic to a single food chain, must be taken into consideration when determining how anthropogenic environmental perturbation affects trophic interactions (Hunter & Price 1992; Jones *et al.* 1997).

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CHAPTER 7

HOST-PLANT AGGREGATION AND PHENOLOGY AFFECT PARASITISM IN EXPERIMENTAL HABITAT PATCHES [e]

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Spatial habitat structure can influence the likelihood of patch colonisation by dispersing individuals; sensitivity to this spatial heterogeneity often varies with trophic position. The resource concentration hypothesis predicts that higher specialist herbivore densities, and by extension their natural enemies, should occur where the habitat, the host-plant, is concentrated in patches. Using a tri-trophic thistle-seed herbivore-parasitoid system we tested whether habitat patch size, isolation and host-plant heterogeneity differentially affected host and parasitoid densities. 240 second-year C. palustre *thistles were transplanted in 24 blocks replicated in two sites, to create a range of habitat patch sizes at increasing distance from a pre-existing source population. Coincident with peak insect oviposition the architecture and the phenological stage (% open inflorescences) were determined for each plant. The numbers of the herbivore* T. conura *and parasitoid* P. elevatus *emerging from each plant were recorded. Patch area had a differential impact according to trophic position. Herbivores increased in numbers in the largest patches while the parasitoid was unaffected, although there was a slight trend for reduced parasitism in larger patches. Isolation of the habitat patch did not affect the herbivore, parasitoid or parasitism rates. Host insect density was a major predictor of parasitoid number and parasitism was inversely density-dependent. The phenological stage of the host-plant directly affected both herbivore and parasitoid populations, and interacted with patch size to increase herbivore densities in the larger patches. The concentration of herbivores in the largest habitat patches, the inverse density-dependent parasitism, and the potential for unstable (CV^2 <1) host-parasitoid dynamics in spatially structured habitat leads us to suggest that these large host-plant aggregations may*

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[e] Draft paper for submission to Ecological Entomology

provide a spatial refuge from parasitoid attack. This refuge most probably arises as a consequence of a differential behavioural response of host and parasitoid to the heterogeneity in the plant distributions.

7.1 Introduction

Metapopulation theory predicts that the presence of a species in a landscape is dependent on the balance between local extinction and colonisation of habitat patches by dispersing individuals (Hanski 1998). Source populations persist in more favourable habitat patches and the probability of colonisation of vacant patches is increased by proximity to these occupied habitat patches (Hanski 1998). The majority of classic metapopulation studies have focussed on the impact of spatial habitat structure on individual species at one trophic level (reviewed in Hanski (1999)); the effect of spatial habitat structure upon interactions between secondary and tertiary trophic levels have been examined in only a few microcosm (Holyoak 2000; Ellner *et al.* 2001; Bonsall *et al.* 2002) and field (Van Nouhuys & Hanski 1999; Weisser 2000; Cronin 2004) studies.

The sensitivity of a species to spatial habitat heterogeneity is often dependent on trophic position. Predators and parasitoids are - compared with herbivores - more prone to extinction as a consequence of anthropogenic habitat fragmentation (Kruess & Tscharntke 1994; Didham *et al.* 1998; Gilbert *et al.* 1998; Davies *et al.* 2000; Spencer 2000). The factors that influence the colonisation of habitats in naturally patchy landscapes vary with trophic position; predators tend to have greater dispersal abilities and thus are likely to be less sensitive than herbivores to spatially sub-divided habitat (Holt 1996; Jones *et al.* 1996; Brodmann *et al.* 1997; Ellner *et al.* 2001 but see Kruess & Tscharntke 2000).

For specialist invertebrate herbivores the habitat patch is most likely represented by the host-plant. Where host-plants are aggregated they represent to specialist herbivores a concentration of a food resource in a habitat patch that varies in size and quality, plant density, and isolation from other patches (Williams *et al.* 2001; Otway *et al.* 2005). The resource concentration hypothesis (Root 1973) suggests that specialist herbivores should attain higher densities where their host-plants are concentrated in patches; dispersing herbivores are more likely to locate and reproduce in, and less likely to leave, such habitat patches (Root 1973; Sheehan & Shelton 1989; Otway *et al.* 2005). Spatially patchy host-plant distributions produce aggregated herbivore populations and such spatial heterogeneity in herbivore populations can have a role in structuring parasitoid population dynamics and influencing parasitism rates (Jones & Hassell 1988; Pacala *et al.* 1990; Hassell *et al.* 1991; Dubbert *et al.* 1998; Umbanhowar *et al.* 2003).

Wider environmental heterogeneity - beyond the interaction with host insect density – may also influence parasitism rates. Habitat patch size and isolation (Maron & Harrison 1997; Doak 2000; Kruess & Tscharntke 2000; Cronin 2004), the identity (Englishloeb *et al.* 1993; Van Nouhuys & Hanski 1999) and density (Cappuccino 1992) of the host's food, the plant community diversity (Vanbergen *et al.* 2006), vegetation height and complexity (Kruess & Tscharntke 2002; Gols *et al.* 2005) and landscape structure (Roland & Taylor 1997; Cappuccino *et al.* 1998; Kruess 2003; Thies *et al.* 2003) are all now understood to have the potential to affect parasitism rates.

Using a tri-trophic system consisting of a thistle (*Cirsium palustre* L.), a seed herbivore (*Tephritis conura* Loew) and a parasitoid (*Pteromalus elevatus* (Walker)) we aimed to test whether habitat patch size, quality and isolation affected herbivore and parasitoid densities, and parasitism rates. Previous study suggested that herbivore and parasitoid differed in their response to host-plant aggregation – the herbivore was unaffected by host-plant distribution whereas parasitism was higher where host-plants were aggregated (Vanbergen *et al.* 2006). To test further the response of this host-parasitoid interaction to habitat spatial structure we established a network of experimental habitat (*C. palustre*) patches. These habitat patches varied in terms of patch size (number of individual *C. palustre*), patch quality (host-plant architecture and phenological stage), and distance from a pre-existing source population.

We hypothesised, firstly, that habitat patch size and isolation would differentially affect patch colonisation by the host and parasitoid, and thus parasitism rates. Secondly, that host-plant heterogeneity would directly and indirectly (via host insect density) affect the parasitoid densities and parasitism rate.

7.2 Method

7.2.1 Tri-trophic system

The marsh thistle *Cirsium palustre* is a multi–stemmed biennial ranging from 50 to 120 cm in height with composite flower-heads clustered at the end of each stem. *Cirsium palustre* tends to have an aggregated dispersion where it occurs naturally (Williams *et al.* 2001). Flowering occurs from early June to mid–September and seed herbivores attack the flower-heads - the most common of which are tephritid flies (Diptera: Tephritidae). The adult tephritid fly inserts its eggs among the florets of recently opened flower-heads and the larva burrows into the flower-head where it feeds on the seeds and receptacle (Janzon 1984; Jones *et al.* 1996). The tephritid *Tephritis conura*, a thistle specialist, is univoltine with gregarious larvae (up to seven conspecific larvae per capitulum) feeding during June and July. The long-lived adult (~9 months) emerges in August to over-winter; mating and oviposition on thistle flowers takes place in the following Spring (Janzon 1984; White 1988; Romstöck-Völkl 1990b). In Britain, *T. conura* has also been recorded feeding on *Cirsium heterophyllum* (L.) Hill (White 1988), a species not seen in the sites studied here. *Pteromalus* (= *Habrocytus*) *elevatus* (Walker) (Hymenoptera: Pteromalidae) a parasitoid of tephritids attacks *T. conura* in the experimental study site (Vanbergen *et al.* 2006). This ectoparasitoid species probes the thistle capitula with its ovipositor and deposits its eggs onto a single host larva; the emerging larvae destroy competitors so that a single parasitoid is reared per host (Hoebeke & Wheeler 1996). Peak *P. elevatus* oviposition (attacking other hosts) is known to occur during early to mid–August (Jones *et al.* 1996). The parasitoid either over-winters within the larval host (yielded from late season *T. conura*) or as an adult (when yielded from early season *T. conura*) (A.J.Vanbergen. *pers.obs*). Identification of *T. conura* was based on White (1988) and *P. elevatus* on Hoebeke & Wheeler (1996).

7.2.2 Experimental field sites and design

240 second year *C. palustre* thistles were transplanted from a nearby field location (Headinch 57° 3.3'N 02° 57.9'W) individually into pots (25cm diameter, 20 cm height) and introduced as part of a randomised block (n = 24 patches) design (Figure 7-1) to two experimental sites (Brathens 57° 4.6'N 02° 32.2'W; Corntulloch 57° 3.9'N 02° 55.0'W). The thistles were introduced prior to flowering and tephritid-parasitoid activity into the experimental sites in April 2004 to enable the plants to acclimate and ensure phenological asynchrony with colonising insects did not confound the experiment (Jones *et al.* 1996). Previous work (Vanbergen *et al.* 2006) mapping thistle distributions identified these two experimental sites as supporting a pre-existing population of *C. palustre* restricted to a single marsh. The two sites supported a high (Brathens) and low (Corntulloch) population density of *T. conura* and *P. elevatus* (Vanbergen *et al.* 2006). Patches of thistles were established at the vertices of a square grid to create a range of habitat patch size classes: small (2 individual plants per patch), medium (4 plants), large (8 plants), extra-large (16 plants) at increasing distance (10, 20 and 40m) from the pre-existing source population of *C. palustre* and associated *T. conura* and *P. elevatus* (Figure 7-1). The distance from the source population of the experimental

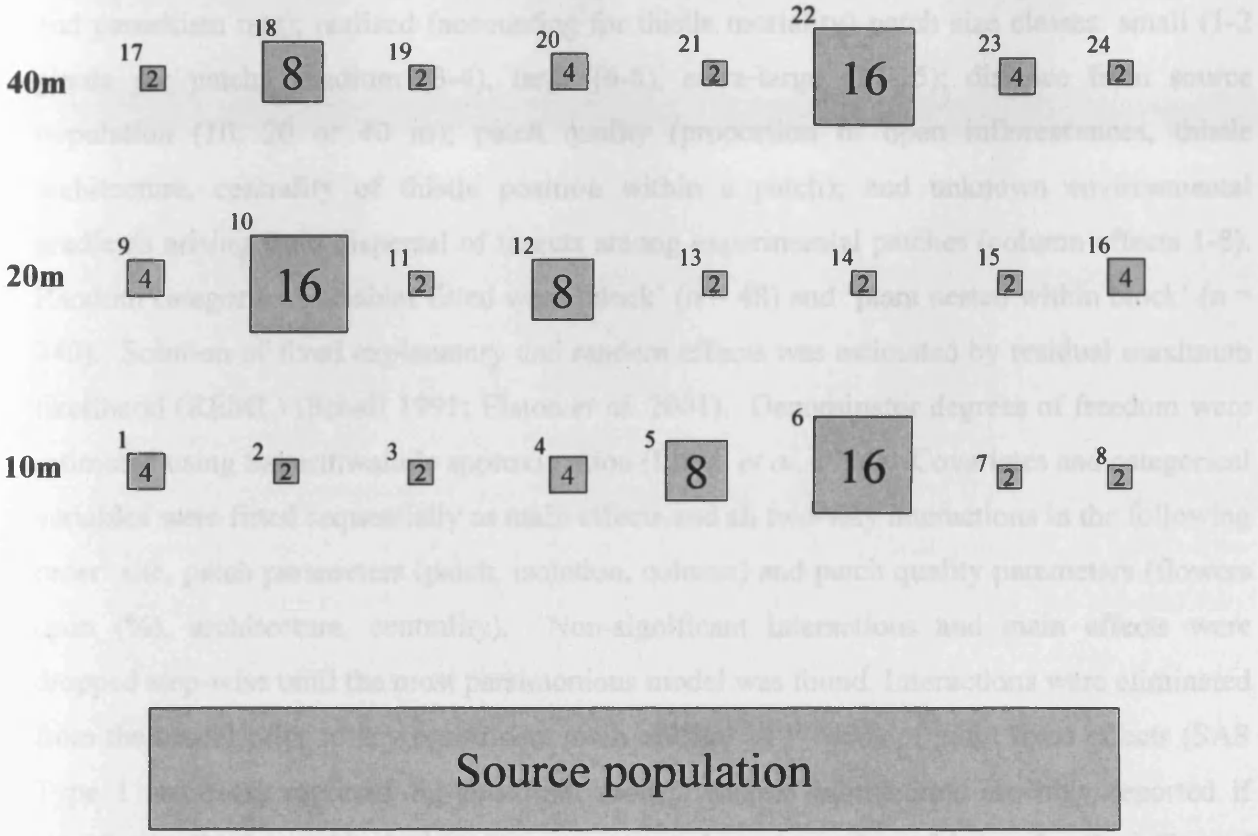
patches was based on knowledge available on the maximum dispersal distances within a site of tephritids (upto 50m) and pteromalid parasitoids (upto 100m) (Jones *et al.* 1996). Replicate potted thistles stood in individual water trays and were watered (1L per plant) weekly to supplement rainfall.

Plate 7.1. Experimental thistle patch at Corntulloch

7.2.3 Tephritid and parasitoid counts

At the end of August 2004, following peak tephritid and parasitoid oviposition (Jones *et al.* 1996), the flower-heads of each individual plant were excised, placed inside Organza bags, and transferred to an outdoor insectary at the Centre for Ecology & Hydrology (CEH) Banchory. Subsequently (September 2004, May 2005) the numbers of *T. conura* and *P. elevatus* emerging from each plant were recorded. Previous work (Vanbergen *et al.* 2006) had shown that this host-parasitoid interaction dominated the *C. palustre* seed head fauna, and other species in this study system were uncommon (e.g. *Palloptera* spp.) or did not influence the *T. conura-P. elevatus* interaction (e.g. *Xyphosia miliaria* Schrank). The total number of host *T. conura* pupae was estimated from the sum of all emerging insects and from this parasitism rates were calculated (number of emerging *P. elevatus* / total number of *T. conura* pupae). This estimate is based on the assumption that larval mortality from other sources (e.g. predation by microlepidopteran larvae) is likely to be insignificant (Romstöck-Völkl 1990b; Vanbergen *et al.* 2006).

Figure 7-1. Schematic diagram of the experimental *C. palustre* habitat patches established to create a range of habitat patch sizes (2,4,8,16 individual plants) at increasing distance (10, 20 and 40m) from the pre-existing source population of *C. palustre* and associated *T. conura* and *P. elevatus* located in a small marsh. The experiment was replicated in two birch woodland sites (host-plants = 120, patches = 24). The number in the upper left hand corner of each patch denotes patch identity.



7.2.4 Host-plant variables

Coincident with peak insect activity (late July) (Jones *et al.* 1996; Vanbergen *et al.* 2006) the proportion of open, inflorescences on each thistle was recorded. Thistle architectural complexity (sum of branches and stems per plant) was also recorded. The number of adjacent thistles was determined for each plant replicate to provide an index of the centrality of each plant within a patch.

7.2.5 Statistical analysis

Data were analysed using generalised linear mixed models (GLMM) (SAS version 8.01, SAS Institute) with replication at two strata: i) the habitat patch (n= 48) to test for patch size and isolation effects, and ii) individual plant (n = 240) to test for patch quality effects. Dependent variables were the count of *T. conura* and *P. elevatus*, and percent parasitism of *T. conura*. Parasitism was modelled as the proportion of emerging *P. elevatus* from the total host pupae per plant. Poisson error distributions with a Log-link were fitted to models of host insect and parasitoid abundance; binomial errors and logit link were applied to parasitism data. Available explanatory data (covariates and categorical variables) were: site (Brathens or Corntulloch); count of emerging host insects (*T. conura*) (for models of parasitoid abundance and parasitism rate); realised (accounting for thistle mortality) patch size classes: small (1-2 plants per patch), medium (3-4), large (6-8), extra-large (13-15); distance from source population (10, 20 or 40 m); patch quality (proportion of open inflorescences, thistle architecture, centrality of thistle position within a patch); and unknown environmental gradients arising from dispersal of insects among experimental patches (column effects 1-8). Random categorical variables fitted were 'block' (n = 48) and 'plant nested within block' (n = 240). Solution of fixed explanatory and random effects was estimated by residual maximum likelihood (REML) (Schall 1991; Elston *et al.* 2001). Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell *et al.* 1996). Covariates and categorical variables were fitted sequentially as main effects and all two-way interactions in the following order: site, patch parameters (patch, isolation, column) and patch quality parameters (flowers open (%), architecture, centrality). Non-significant interactions and main effects were dropped step-wise until the most parsimonious model was found. Interactions were eliminated from the model prior to any constituent main effects; all F-ratios of main fixed effects (SAS Type 1 tests) are reported for this final model whereas interactions are only reported if significant. Partial residual plots were constructed to show the evidence for the effect of particular covariates, and include a fitted line to show the slopes, but not necessarily the correct intercept, of the relationships.

The square of the coefficient of variation (CV^2) gives an approximation of the stability of host-parasitoid dynamics: the CV^2 rule states that the interaction between the host and parasitoid will be stable if the coefficient of variation (CV^2) of searching parasitoids per patch is greater than 1 (Pacala *et al.* 1990; Hassell *et al.* 1991). The $CV^2>1$ rule was used to test for the potential contribution of observed heterogeneity to stable host-parasitoid dynamics (Hassell 2000). Because of practical difficulties inherent in collecting field data on the distribution of searching adult parasitoids per host patch the CV^2 was estimated from the distribution of parasitism rather than searching parasitoid adults (Hassell 2000). The number of parasitoids per patch was weighted by the estimate of host pupal density (sum of emerging parasitoids and hosts) to control for the scale-dependent sensitivity of the CV^2 criterion (Hassell 2000). A caveat in this case is that repeated sampling over many years would be needed for any conclusions on the stability of the studied host-parasitoid interaction - inferred from the $CV^2>1$ rule - to be fully justified (Hassell 2000). The $CV^2>1$ rule, in this case, provides a means of evaluating the potential for habitat heterogeneity to influence percentage parasitism (Hassell 2000). The $CV^2>1$ rule was tested at the level of the host-plant (n = 217) and the patch size classes (extra-large: n = 6, large: n = 6, medium: n = 12, small: n = 24).

7.3 Results

7.3.1 Influence of woodland sites

A total of 3430 *T. conura* and 3100 *P. elevatus* emerged from the experimental habitat patches in one (*T. conura*: August-September 2004) and two (*P. elevatus*: August-September 2004, April-May 2005) waves. The only other insect species yielded from this experiment was another tephritid (*X. miliaria*) of much lower abundance (Corntulloch = 5 individuals, Brathens = 60) and previously shown (Vanbergen *et al.* 2006) to be of little importance to the studied host-parasitoid interaction. As shown in previous work (Vanbergen *et al.* 2006) there was a strong influence of woodland site on the numbers recorded from the experimental thistle patches of *T.conura* (Brathens: $\bar{x}$ = 9.4 *sd* = 12.0, Corntulloch: $\bar{x}$ = 22.7 *sd* = 17.4, Table 7-1) and *P. elevatus* (Brathens: $\bar{x}$ = 0.9 *sd* = 2.2, Corntulloch $\bar{x}$ = 28.6 *sd* = 22.9, Table 7-1). Proportional parasitism was similarly affected by site level differences (Brathens: $\bar{x}$ = 0.10 *sd* = 0.27, Corntulloch: $\bar{x}$ = 0.55 *sd* = 0.19, Table 7-1). Thereafter all remaining categorical variables and covariates were tested after controlling for this significant site-level variance.

7.3.2 Habitat patch size and isolation: Influence on herbivore and parasitoid populations

The size of the habitat patch was overall a significant predictor of *T. conura* abundance, the largest patches yielding more *T. conura* individuals than the smaller patches (Table 7-1, Figure 7-2). Habitat patch size did not have a statistically significant effect upon parasitoid abundance or proportional parasitism (Table 7-1, Figure 7-2); nevertheless, with increasing patch size there appeared to be a declining mean parasitism rate (Figure 7-2). The numbers of *T. conura* or *P. elevatus* yielded from a habitat patch, and the proportional parasitism of *T. conura* were unaffected by the isolation of the habitat patch, tested as the distance (10, 20, 40m) of the habitat patch from the source population (Table 7-1). Furthermore, there were no significant column effects on the numbers of *T. conura* and *P. elevatus,* or proportional parasitism (Table 7-1); therefore this study provides little evidence for significant gradients in insect distribution between experimental habitat patches.

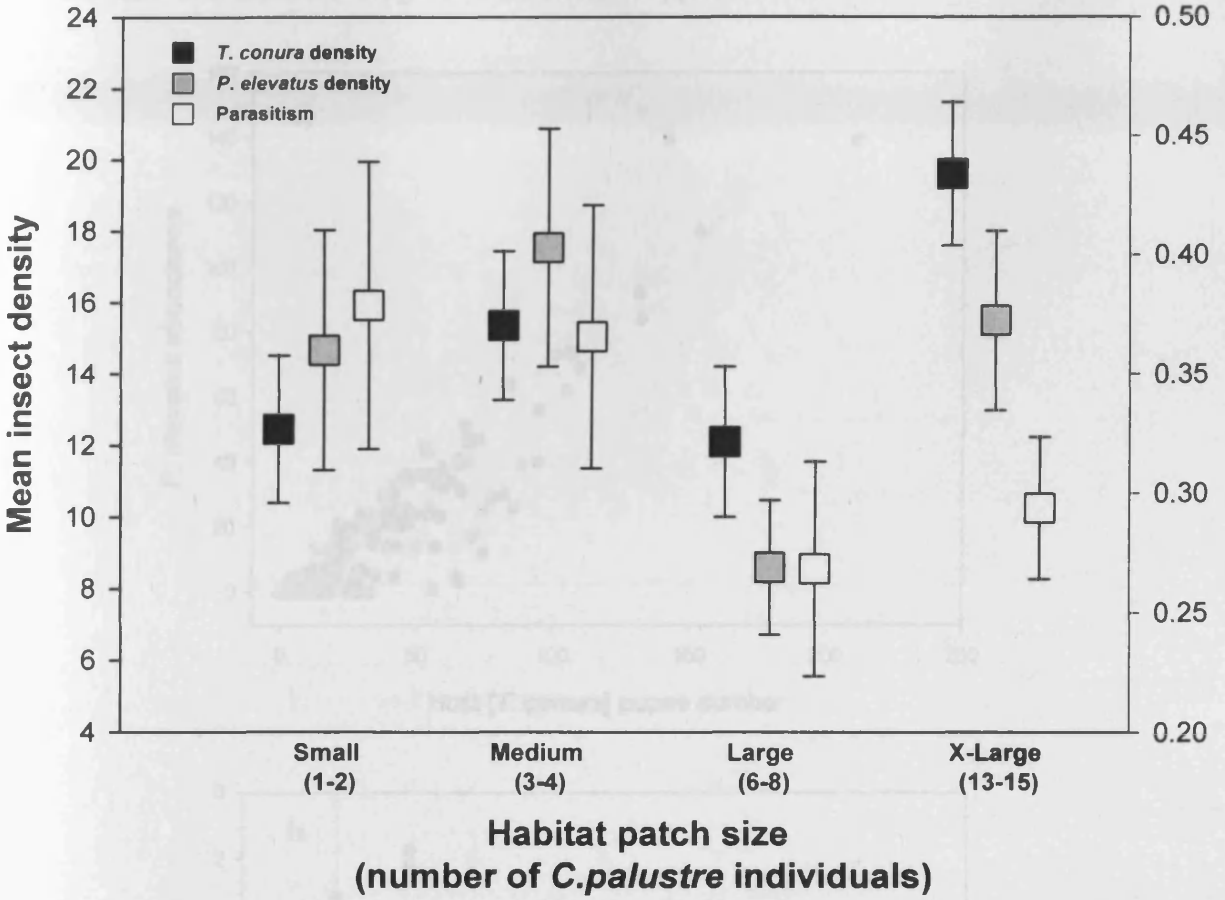
Table 7-1. F-ratios of main fixed effects (SAS Type 1 tests) from a GLMM of the factors affecting the numbers of an herbivore *T. conura*, its parasitoid *P. elevatus* and percentage parasitism. Poisson error distributions with a Log-link were fitted to models of host insect and parasitoid abundance; Binomial errors and logit-link were applied to parasitism data. Solution of fixed explanatory and random effects was estimated by residual maximum likelihood (REML). Denominator degrees of freedom were estimated using Satterthwaite's approximation.

	***T. conura* (n)**		***P. elevatus* (n)**		**Parasitism (%)**	
Predictor	**F** $_{(d.f.)}$	**P**	**F** $_{(d.f.)}$	**P**	**F** $_{(d.f.)}$	**P**
Site	**41.81** $_{(1, 28)}$	**< 0.0001**	**238.72**$_{(1, 29)}$	**< 0.0001**	**205.89**$_{(1, 27)}$	**< 0.0001**
Host density	-	-	**12.29**$_{(1, 212)}$	**0.0006**	**30. 78**$_{(1, 158)}$	**< 0.0001**
Patch size	**3.45** $_{(3, 29)}$	**0.03**	0.69$_{(3, 17)}$	0.57	0.67$_{(3, 7)}$	0.60
Patch distance	0.58 $_{(2, 31)}$	0.56	0.06 $_{(2,18)}$	0.95	0.40 $_{(7, 7)}$	0.68
Column effect	1.28 $_{(7, 31)}$	0.29	0.87$_{(7, 19)}$	0.55	0.38 $_{(7, 7)}$	0.89
Plant architecture	0.16 $_{(1, 173)}$	0.69	0.04$_{(1, 140)}$	0.84	0.02 $_{(1, 84)}$	0.90
Infloresences (n/N)	**14.44** $_{(1, 176)}$	**0.0002**	**8.25** $_{(1,212)}$	**0.0045**	**6.51** $_{(1, 134)}$	**0.01**
Plant centrality	0.26 $_{(1, 161)}$	0.61	0.01$_{(1, 106)}$	0.91	0.05$_{(1, 40)}$	0.82

7.3.3 Habitat patch quality: Influence on herbivore populations

The quality of the habitat patches was a significant predictor of colonisation by *T. conura*. After controlling for the significant effect of site and habitat patch size the proportion of flowers supported by a thistle was positively related to the abundance of *T. conura* (Table 7-1, Figure7-4a). The strength of this relationship was increased by the significant interaction with habitat patch size (Figure 7-5, $F_{3,\ 179} = 3.63$, $p = 0.01$). The slope of the relationship between *T. conura* density and the proportion of open flowers was significantly different from zero for large ($b = 4.94$, $p < 0.0001$) and extra –large patches ($b = 1.52$, $p = 0.0195$), but not for the small ($b = 1.18$, $p = 0.16$) and medium sized patches ($b = 0.37$, $p = 0.76$) (Figure 7-5). There was no influence of habitat patch size on the proportion of open flowers per thistle ($F_{3,\ 32} = 1.37$, $p = 0.27$), even after controlling for site-level differences in the proportion of open flowers (Brathens: $\bar{x} = 0.62$ $s = 0.20$, Corntulloch: $\bar{x} = 0.74$ $s = 0.14$; $F_{1,\ 38} = 14.90$, $p = 0.0004$). The architecture of individual thistles or the position (central or edge) of the thistle within a patch had no affect on *T. conura* density (Table 7-1).

Figure 7-2. The effect of patch size classes on the mean (± SE) abundance of *T. conura* ($F_{3, 29} = 3.45$, $P = 0.03$), *P. elevatus* ($F_{3, 17} = 0.69$, $P = 0.57$) and the proportion of parasitized *T. conura* pupae ($F_{3, 7} = 0.67$, $P = 0.60$). Data were analysed with GLMM (REML) with Poisson errors and log link for count data and binomial errors and logit link for parasitism data. Degrees of freedom were estimated using the Satterthwaite's approximation.



7.3.4 Host insect density: Influence on parasitoid populations

The abundance of *P. elevatus* was strongly and positively correlated to the total number of available host pupae (Figure 7-3a), even after controlling for site-level differences (Table 7-1). This relationship was, however, asymmetric (<1:1, Figure 7-3a) resulting in the percentage parasitism (parasitoid emergence / total host pupae) being inversely proportional to the density of emerging host *T. conura* (Figure 7-3b, Table 7-1). At the host-plant level percentage parasitism level with the potential for stable dynamics ($CV^2 = 1.05$), but this potential for stability disappeared when spatial heterogeneity in habitat patch structure was introduced (CV^2: extra-large = 0.66, large = 0.62, medium = 0.90, small = 0.87). It is notable, however, that the host-parasitoid interaction is closer to the values required to infer stability in the smaller host-plant aggregations.

Figure 7-3. Relationship between a) *P. elevatus* density per host-plant and total host pupal number (sum of emerging *T. conura* and *P. elevatus*) (Pearson correlation coefficent = 0.91, $P < 0.001$) and b) partial residual percentage parasitism of *T. conura* on the linear predictor scale in response to the density of emerging *T. conura* per host-plant ($F_{1, 158}$ =30. 78, P <0.0001). Percentage parasitism data were analysed and lines fitted with a GLMM (REML) with binomial errors and logit link. Degrees of freedom were estimated using the Satterthwaite's approximation.

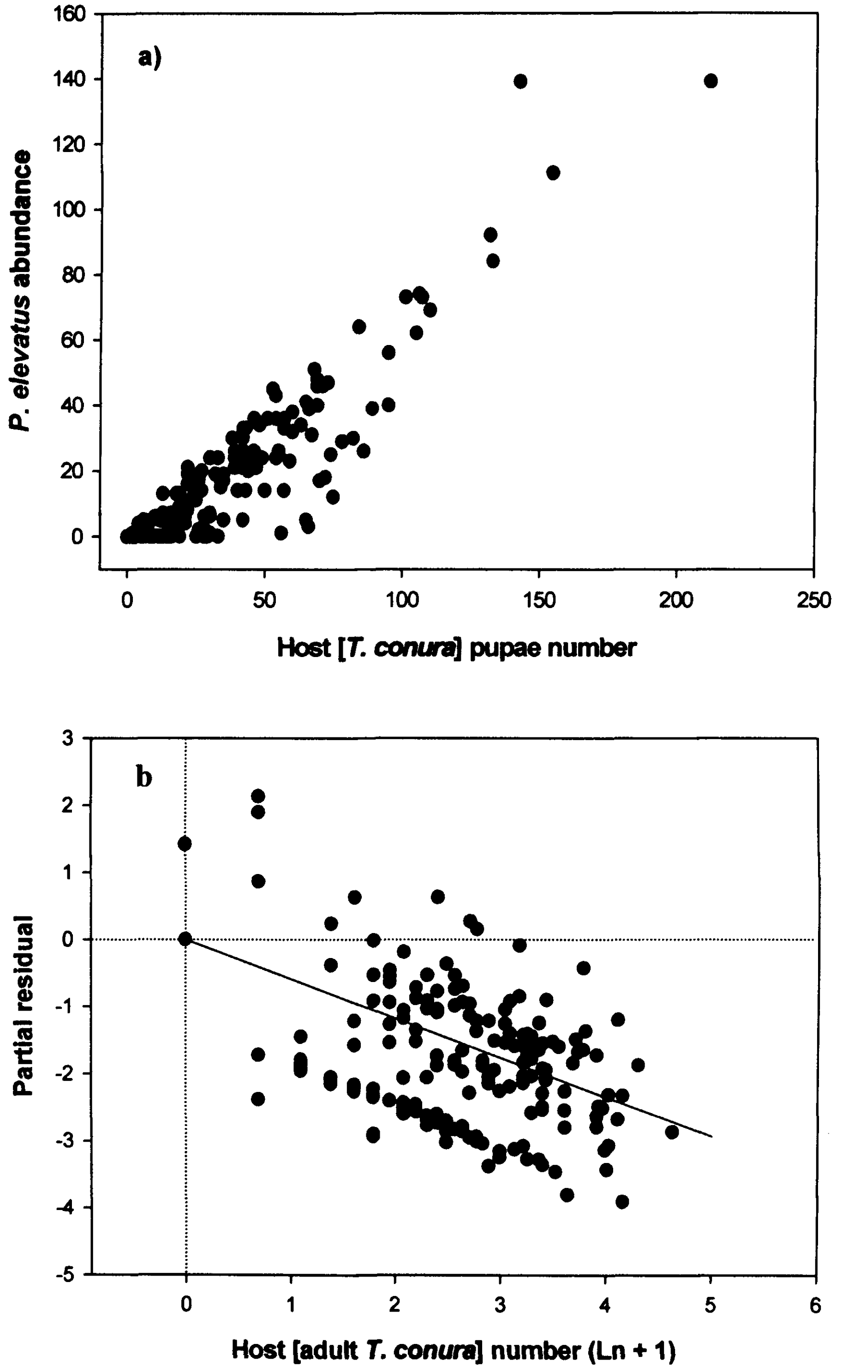


Figure 7-4. Relationship between the proportion of open inflorescences per host-plant and a) partial residual abundance of *T. conura* ($F_{1,176} = 14.44$, $P = 0.0002$) and b) partial residual proportional parasitism ($F_{1,134} = 6.51$, $P = 0.01$) on the linear predictor scale. Data were analysed and lines fitted with GLMM (REML) with Poisson errors and log link for count data and binomial errors and logit link for parasitism data. Degrees of freedom were estimated using the Satterthwaite's approximation.

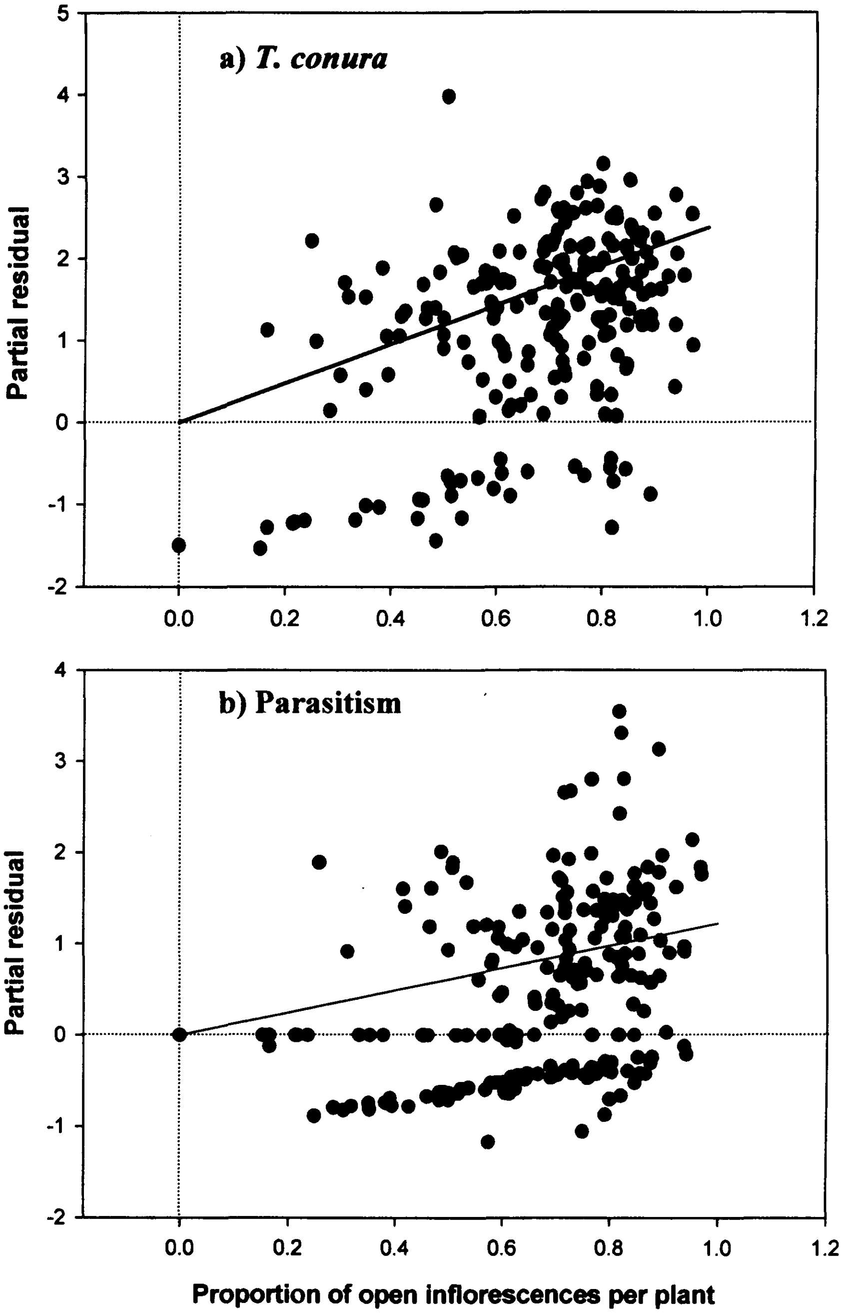
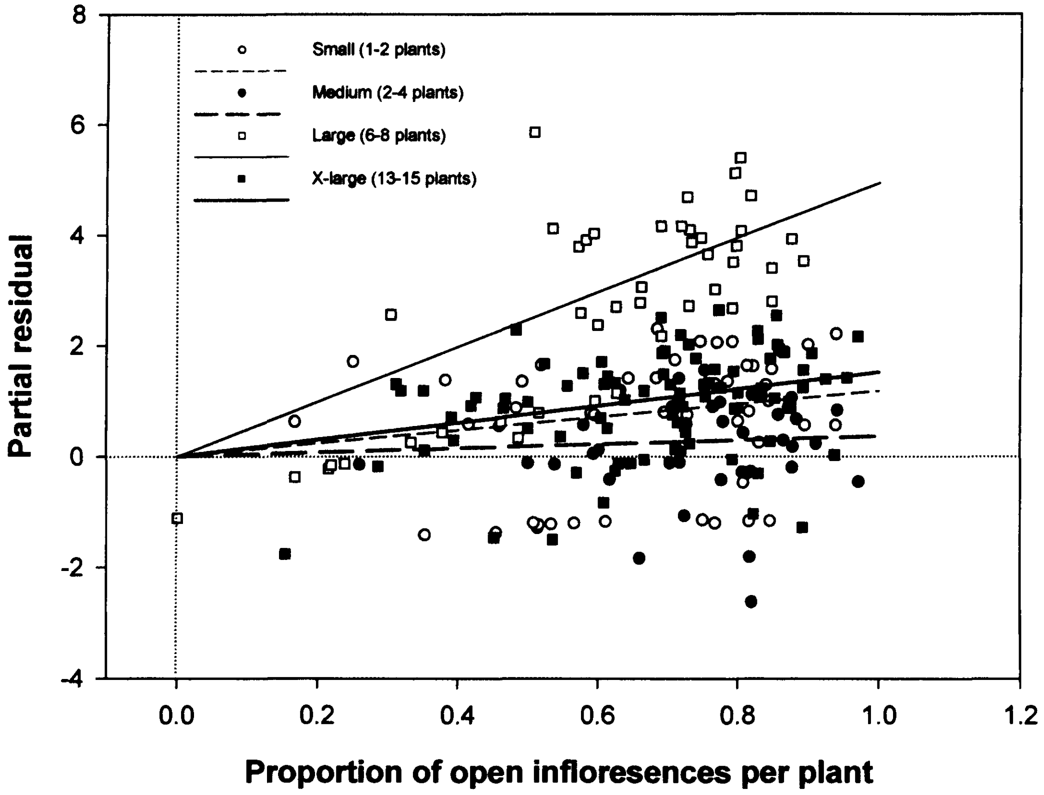


Figure 7-5. Effect on partial residual *T. conura* abundance of the interaction between habitat patch size class and the proportion of open inflorescences per host-plant ($F_{3,179} = 3.63$, $p = 0.01$). Slopes of the relationship for extra-large ($b = 1.52$, $p = 0.0195$), large ($b = 4.94$, $p < 0.0001$), medium ($b = 0.37$, $p = 0.76$) and small ($b = 1.18$, $p = 0.16$) patches. Data were analysed and lines fitted with GLMM (REML) with Poisson errors and log link for count data. Degrees of freedom were estimated using the Satterthwaites approximation.



7.3.5 Habitat patch quality: Influence on parasitoid populations

P. elevatus abundance and percentage parasitism was - after accounting for host insect number and site differences - positively related to the proportion of open inflorescences per plant (Table 7-1, Figure 7-4b), but was unaffected by thistle architecture (Table 7-1) or position within a habitat patch (Table 7-1). Thus over and above the effect of host insect density there remained an effect of patch quality, specifically the proportion of open flowers available for oviposition by the searching parasitoid, on parasitoid number and percentage parasitism.

7.4 Discussion

There was some evidence that habitat patch size did have a differential impact on the secondary and tertiary trophic levels of the studied food chain: the herbivore *T. conura* increased significantly in numbers in the very largest habitat patch class, while parasitoid numbers and parasitism rates were independent of the habitat patch size. The isolation of the habitat patch from the source population, contrary to our prediction and published evidence elsewhere (Kruess & Tscharntke 1994; Maron & Harrison 1997; Doak 2000; Cronin 2004), did not influence herbivore and parasitoid abundance or percentage parasitism. The experimental *C. palustre* patch sizes, therefore, established a gradient in larval resources (*C. palustre* seeds, *T. conura* larvae) for the dispersing seed herbivore *T. conura* but not for its parasitoid *P. elevatus*. This lack of a parasitoid response to host-plant patch size contrasts with other studies showing strong bottom-up effects on parasitism: Sheehan & Shelton (1989) in a study of aphid parasitism showing longer parasitoid residence times in larger habitat patches and where prey density was greater; Dubbert *et al.* (1998) similarly showed a positive correlation between parasitism and the proportion of plant shoots attacked by host insects – it being easier to locate and parasitise hosts in areas of high host density.

Mechanisms explaining the influence of host-plant variables (e.g. patch size) on parasitism rates are not always clear but may involve changes in behaviour or microclimate (Sheehan & Shelton 1989) or reflect the different perception of habitat structure according to dispersal abilities or range sizes (Holt 1996; Jones *et al.* 1996). It is possible in this case the parasitoid simply does not perceive the experimental habitat structure, due to the grain of the spatial habitat heterogeneity being within the range of between-plant dispersal shown for *P. elevatus* (Jones *et al.* 1996). Similarly the habitat patches may not have been sufficiently isolated from each other and the source habitat to have a significant influence on patch colonisation by the dispersing insects. A previous study (Jones *et al.* 1996) showed maximum dispersal distance between *C. palustre* thistles (within a single site) was 50m for another tephritid host species and upto 100m for *P.elevatus*; previous work on *T. conura* suggests this species has the potential to disperse to host-plants up to 1.5 km away from the point of emergence (Romstöck-Völkl 1990a). The potential for step-wise insect dispersal among patches to mitigate the effect of isolation does not seem a likely alternative explanation because no significant column effects were detected, together with the lack of a patch isolation effect, means that in this experiment we have little evidence of habitat structure impacting on insect dispersal. The differential impact of habitat patch size on the host and parasitoid also contrasts with previous work in this system (Vanbergen *et al.* 2006) which showed the opposite pattern of *T. conura* being insensitive to the host-plant distribution and higher parasitism rates where host-plants were clumped. The reason for this difference may be that the earlier study mapped thistles in a 100m^2 with thistle patches defined at a resolution of 5m^2 and the largest of these patches was never composed of more than eight individual plants. The size and density of the experimental thistle patches in this paper was therefore greater than that observed in the previous study, which may contribute to the contrasting results.

While patch size and isolation either partly or did not influence herbivore abundance and parasitism, the availability of the larval resource (seeds or host larvae) mediated via the phenological stage of the host-plant is an important predictor of patch colonisation by the dispersing host insects and parasitoids. The proportion of open inflorescences per plant was a significant positive correlate of the densities of herbivore and parasitoid, and percentage parasitism. This confirms that for tephritid seed herbivores, access to the larval seed resource is restricted by the phenological stage of thistle flower-heads, requiring budburst to allow oviposition (Romstöck-Völkl 1990b; Williams *et al.* 2001; Vanbergen *et al.* 2006).

The positive influence of advanced plant phenology on *T. conura* abundance is modified by the size of the host-plant aggregation: in the larger patches the slope of the correlation between herbivore abundance and plant phenology is significantly steeper compared to where host-plants occur in smaller patches. Habitat patch size had no direct effect on the proportion of open inflorescences, and thus did not affect the availability of the seed resource. The inference from this interaction between patch size and plant phenology is that larger habitat patches elicit a behavioural change in the ovipositing herbivore, perhaps reducing the likelihood of leaving the larger habitat patches once located (Sheehan & Shelton 1989). *T. conura* oviposits randomly within a host-plant although with the tendancy to avoid buds with large numbers of eggs (Romstöck-Völkl 1990a). An ovipositing female is perhaps likely to reside longer in large host-plant patches that provide a greater density of available oviposition sites compared to patches composed of one or to individual plants rapidly occupied by conspecifics.

The phenological stage of the host-plant was also a significant, positive predictor of parasitoid abundance and parasitism rates. This effect of host-plant heterogeneity on parasitism was seen after controlling for the effect of *T. conura* density per plant, and thus also the effect of plant phenology on the host insect. There was therefore a direct, host-plant mediated effect on the availability of the resource to searching parasitoids with consequences for parasitism rates. The phenological stage of the developing flower-head is known to influence the ability of other *Pteromalus* parasitoid species attacking *T. conura* larvae feeding on *C. heterophyllum* with larvae at the centre of flowerheads or in mature, larger flowerheads finding a structural refuge from parasitism (Romstöck-Völkl 1990a). The observed correlation with *C. palustre* host-plant phenology in this current paper may represent the presence of a similar phenological attack window.

Parasitoid abundance was positively correlated to the estimated total count of host insects but this relationship was asymmetric (<1:1) with parasitoid numbers lagging behind at high host insect densities. This led, as seen in other studies (Stiling 1987; Lozano *et al.* 1996; Williams *et al.* 2001), to parasitism rates being inversely related to host density. Inverse density-dependent patterns in parasitism are often a result of interference among parasitoids or constraints set by handling time (Waage 1983; Visser *et al.* 1999). In this present study differential aggregative response of herbivore and parasitoid to spatial heterogeneity in the host insect food-plant may be driving this inverse parasitism rate. Firstly, there is a slight, albeit not statistically significant decline in parasitoid numbers and percentage parasitism accompanying the rise in host insect density within the largest habitat patches. Secondly, when evaluated against the $CV^2 > 1$ rule the habitat patch size influenced the potential stability of this host-parasitoid interaction. The heterogeneity in parasitism has the potential for stable host-parasitoid dynamics at the scale of individual host plants, but this breaks down at the patch scale. Furthermore, there is a trend towards increasing potential for stable host-parasitoid dynamics with decreasing habitat patch size. It is important to note, however, that whether the host-parasitoid dynamic is stable can only be properly ascertained by sampling over multiple years (Hassell 2000). Furthermore, the presence of an alternative host tephritid (*X. miliaria*) - while deemed insignificant at the point in space and time in this paper and others (Vanbergen *et al.* 2006) – might nevertheless have a role in the host-parasitoid dynamics when examined over longer timescales (Hassell 2000).

Taken together these data, caveats acknowledged, suggest that the herbivore *T. conura* might have a spatial refuge from parasitism where the host-plants are aggregated at higher densities (Jeffries & Lawton 1984; Williams *et al.* 2001 but see Begon *et al.* 1995). Potentially this refuge may arise from the greater architectural complexity (arising from the tangle of stalks and branches) of the large patches interfering with parasitoid searching and host location efficacy (Gingras & Boivin 2002; Gols *et al.* 2005), but the lack of an effect of thistle architecture on parasitism does not support this hypothesis. Structural refuges from parasitism within flower-heads are known to occur when *T. conura* attacks *C. heterophyllum* (Romstöck-Völkl 1990b), and it is possible such refuges at the fine-scale of the flower-head may contribute to the observed inverse density dependence. Our data suggest it is perhaps more probable that the spatial refuge arises as a consequence of the differential response of the herbivore and parasitoid to habitat patch sizes. This difference could be attributed to altered dispersal behaviour, in this case of the herbivore, with patch size (Sheehan & Shelton 1989); or differences between host and parasitoid in the scale at which habitat structure is perceived due to greater mobility of the higher trophic level (Jones *et al.* 1996; Brodmann *et al.* 1997; Ellner *et al.* 2001). The insensitivity of *P. elevatus* to host-plant spatial heterogeneity contrasts with recent work demonstrating that density and spatial patchiness in the trophic level underpinning the host can influence parasitism rates (Cappuccino 1992; Roland & Taylor 1997; Vanbergen *et al.* 2006; Appendix IV).

Resource availability governed by host-plant heterogeneity in phenology affects both herbivore and parasitoid densities. The differential impact of plant patch size on this relationship for hosts but not parasitoids, together with an overall lack of sensitivity to patch size by dispersing parasitoids, leads to a spatial refuge from parasitism in larger habitat patches. Spatial heterogeneity at the primary trophic level can structure interactions between secondary and tertiary trophic levels.

Acknowledgments

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CHAPTER 8

DISCUSSION

In this thesis the influence of ecological heterogeneity on invertebrate diversity, trophic guild structure, and species interactions was assessed from landscape to host-plant scales. The large and pervasive influence of human activities, mediated via habitat and plant assemblage heterogeneity, on invertebrate diversity and species interactions is demonstrated to occur at both landscape and habitat scales.

Landscape scale patterns in land-use were shown to have a role in governing the diversity of species that operate at much finer spatial scales. Large-scale variation in the cover of forest and spatial heterogeneity of the landscape was strongly correlated with the diversity of both epigeal beetles and soil fauna. This finding is part of a growing number of studies that demonstrate that coarse-scale environmental gradients have a major role in structuring soil faunal diversity (Chust *et al.* 2003; Chust *et al.* 2004; Dauber *et al.* 2005; Joschko *et al.* 2006), as well as above-ground insects (Steffan-Dewenter *et al.* 2002; Purtauf *et al.* 2005). This thesis showed that land-use can generate landscapes of varying habitat heterogeneity and, while not explicit here, one possible explanation is that this spatial habitat structure will - over time - affect soil faunal diversity via active and passive dispersal (Ojala & Huhta 2001; Dunger *et al.* 2002; Ims *et al.* 2004) and differential population persistence among habitat patches of varying quality e.g. abiotic gradients, disturbance from tillage (Hanski 1999; Ims *et al.* 2004; Bardgett 2005). Whether this large-scale ecological heterogeneity affected the number of species or individuals, and the shape of the relationship, was dependent on the taxonomic identity. For example, at landscape scales carabid beetle and soil fauna diversity were respectively negatively and quadratically correlated with the proportion of forest cover; collembola abundance was negatively and lumbricid abundance positively correlated with the spatial patchiness of the landscape. Overall these findings illustrate that coarse-scale patterns in land-use can have a role in structuring invertebrate communities, even for species that interact with each other, and the environment, at finer spatial scales.

One-way by which land-use changes to landscape structure may affect invertebrate diversity is through changes to plant diversity. Correlation between above-ground and soil animal diversity, however, is uncommon or tends to be weak (Hooper *et al.* 2000; Wardle *et al.* 2003; Armbrecht *et al.* 2004). In this study where such correlations were found – although once again the response varied with taxonomic identity – they tended to be highly significant. Carabid beetle diversity was independent of plant diversity, while lumbricid worms and collembola were highly correlated with forb and tree diversity respectively. That carabids were insensitive to plant diversity is perhaps unsurprising given they are predominantly a predatory taxon, and thus by virtue of their trophic rank, only indirectly connected to the primary trophic level. The highly significant relationship between collembola and tree species richness is presumably a reflection of the large role in which trees have in shaping the amount and diversity of the litter resource underpinning collembola assemblages (Hasegawa 2002, De Deyn *et al.* 2004, Salamon *et al.* 2006). Evidence of the importance of the litter resource to collembola is seen in the negative correlation between collembola abundance and the declining amount of litter at the soil surface as the landscapes become less forested. In contrast, lumbricid worm abundance increased as forb cover increased, litter cover decreased and soil pH rose, a reflection of the adaptation of the majority of lumbricid worm species to open, grassland environments and more neutral soils (Wardle 2002; Bardgett 2005).

It was impossible due to limitations in the study design of Chapters 3 & 4 arising from wider project objectives (e.g.the lack of replicate Scottish land-use gradients reflected the pan-European replication of the wider EU FP5 BioAssess project) to disentangle (e.g. with multivariate regression) the relative importance of different factors structuring invertebrate diversity. Moreover, because the study was purely correlative it is not possible to determine whether the invertebrate assemblages were responding directly to landscape structure or to changing plant diversity along the land-use gradient or other unknown gradients. Controlled experimentation is, however, often not possible or impractical when examining large-scale ecological questions and multivariate environmental gradients, hence it was not possible to separate cause and effect to identify the ultimate factor structuring invertebrate diversity in these landscapes. Despite these statistical shortcomings these observational data can lead to hypotheses to be tested with further observations and experiments at more manageable spatial scales. In this thesis the landscape-scale observations of the factors (e.g. plant diversity, forest cover) structuring invertebrate communities along a land-use gradient led to a study of how a specific anthropogenic land-use, cattle grazing, influenced plant density, diversity and architecture to impact on higher trophic levels (herbivores, predators, parasitoids).

Cattle in birch woodlands act as ecosystem engineers (Jones *et al.* 1997) altering the habitat to produce an architecturally and compositionally distinct plant community in the woodland understorey. This disturbance of semi-natural woodlands led, in grazed woods, to a decline in the species richness and abundance of generalist secondary consumers across a range of invertebrate taxa, but left obligate herbivores unaffected - consistent with the hypothesis that different trophic levels respond differently to ecological heterogeneity (Holt 1996; Kruess & Tscharntke 2000; Thies *et al.* 2003; Purtuaf *et al.* 2005). This loss of secondary consumers was correlated with a reduction in the height of understorey vegetation, and the concomitant increase in plant diversity. The mechanisms via which these grazing-dependent changes in habitat structure and diversity occur are not, in the absence of further experimental manipulations, clear from these data. The changes to the plant assemblage are hypothesised to be driven either singly or in combination by grazing, dunging and trampling affecting interspecific competition and producing niche space (Hobbs 1996; Pykala 2003; Pakeman 2004); while the loss of invertebrate predators is hypothesised to be a function of the loss of niche space with the reduction in the vertical height of the grazed sward (Gibson *et al.* 1992b, Kruess & Tscharntke 2002).

The response to grazing from a specialist insect herbivore *Tephritis conura* and its parasitoid enemy *Pteromalus elevatus* contrasted with that of generalist secondary consumers in this system. Both the herbivore and parasitoid densities, and parasitism rates were positively affected by the presence of grazing cattle. *Tephritis conura* density was positively correlated to the higher plant, particularly forb, diversity in the grazed habitat, and this habitat modification both cascaded up to the parasitoid (via host density) and directly affected the parasitoid density and increase parasitism rates. Specialist phytophages and parasitoid species are more often negatively affected by disturbance due to their narrow host resource base making them vulnerable to extinction (Golden & Crist 1999, Komonen *et al.* 2000, Kruess & Tscharntke 2000, 2002). This thesis, therefore, provides a rare example of how two specialist (stenophagous host ranges) species - one of which is a parasitoid - are positively affected by anthropogenic disturbance. The mechanism by which the grazing-driven habitat modification affected both herbivore and parasitoid populations is, however, not explicit from these data. Grazing had no impact on the thistle host-plant underpinning this interaction thus a conventional bottom-up cascade via the host-plant to the larval insects can be excluded. The correlation with the floral diversity may indicate that an increase in nectar resources could be having a positive effect on the adult herbivores and parasitoids, perhaps via adult nectar feeding promoting adult longevity or fecundity (Jervis 1998, Heimpel & Jervis 2005).

Although these species can be considered to be specialists in the larval stage, once adults both the tephritids and the parasitoid function as generalist nectar feeders. This research, therefore, also highlights the importance of considering the age-structure of populations when assessing how species interact, and respond to environmental heterogeneity (e.g. Reeve 1994).

Independent of anthropogenic habitat heterogeneity, the work on the thistle-herbivore-parasitoid system revealed that natural heterogeneity at the host–plant scale also affected this antagonistic species interaction (Strong *et al.* 1984). The phenological stage of the host-plant was an important predictor of both herbivore and parasitoid densities: bud-burst determined whether the herbivore could successfully oviposit into the larval habitat and thus also limited the availability of host-larvae to the parasitoid. The impact of experimental host-plant patch size was dependent on trophic position: the largest patches supported the greatest herbivore densities but the parasitoid was unaffected by this spatial habitat structure supporting what is understood about the contrasting sensitivity of species occupying different trophic positions to environmental heterogeneity (Holt 1996; Gilbert *et al.* 1998; Davies *et al.* 2000; Thies *et al.* 2003, Purtauf *et al.* 2005). These large host-plant aggregations may provide a refuge from parasitism, and evidence was provided that this refuge may arise as a result of the differential response of herbivore and parasitoid to habitat structure (Jones *et al.* 1996; Brodmann *et al.* 1997; Ellner *et al.* 2001). The positive relationship between the phenological stage of the host-plant and herbivore densities was significantly enhanced in the larger host plant aggregations, one possible reason might be that the tephritid herbivores having located a large host-plant patch were less likely to leave it, compared to isolated plants or small plant patches (Sheehan & Shelton 1989). This inferred behavioural shift coupled with the lack of a response by the parasitoid to habitat structure meant, overall, that parasitism was inversely density-dependent (Stiling 1987; Williams *et al.* 2001), and that the potential for stable (CV^2 >1) host-parasitoid dynamics was reduced when the host-plant habitat was spatially structured (Ellner *et al.* 2001).

This thesis demonstrated the possibility of human activities indirectly via the plant communities affecting the diversity and population densities of invertebrate assemblages. Evidence for correlations between diversity at the primary trophic level and consumers is mixed (Siemann *et al.* 1998; Wardle *et al.* 2003; Woodcock *et al.* 2005), with stronger evidence that it is plant species identity and not diversity *per se* that is important in shaping the diversity of higher trophic levels (Wardle *et al.* 2003; De Deyn *et al.* 2004). Evidence is provided in this thesis that plant diversity *per se* can be highly correlated with invertebrate species richness below-ground, and the abundance of generalist predators, host-parasitoid populations, and the strength of parasitism, above-ground. A potential mechanism linking plant diversity to these higher trophic levels (while needing experimental verification) is postulated to be via the effect of plant diversity on the consumer resource base. Elevated plant diversity may increase the diversity of the consumer resources either providing additional niches (Hansen 2000) and contributing to consumer diversity - as in the case of collembola diversity - or by promoting population-level performance, and perhaps increasing fitness, as in the adult stages of the host-parasitoid interaction (Heimpel & Jervis 2005).

The potential for anthropogenic disturbance to semi-natural habitat to alter not only the diversity and guild structure of invertebrate communities, but also interactions between insect species is shown in this study. This supports other studies (Vazquez & Simberloff 2003; Kruess & Tscharntke 2002b) that have found that antagonistic and mutualistic interactions in other systems are similarly affected by agricultural disturbance. The evidence provided by this thesis suggests the response of species to ecological heterogeneity arising from anthropogenic disturbance or land-use may be positive, negative or idiosyncratic. This variability can partly be explained by differences due to the trophic position of the different species studied here, for example the contrasting sensitivity of primary and secondary consumers to grazing-dependent habitat heterogeneity, and is in agreement with many other studies which show greater susceptibility of higher trophic levels to habitat heterogeneity and other disturbances (e.g. Gilbert *et al.* 1998; Davies *et al.* 2000; Kruess & Tscharntke 2000; Thies *et al.* 2003, Purtauf *et al.* 2005). It is important to note, however, that trophic guild is not always a reliable guide: in this study, species within a guild (two tephritid seed herbivores) responded differently to the same grazing–driven heterogeneity for unknown reasons. Such within trophic level responses are often related to differences in specific ecology (Steffan-Dewenter & Tscarntke 2000; Steffan-Dewenter *et al.* 2002), while the life-history differences between the studied tephritids are not obvious (e.g. similar host-ranges) this remains a possible explanation for the contrasting pattern observed here.

The sensitivity of parasitoids and parasitism rates, an important ecological process, to ecological heterogeneity has been shown to extend beyond variation in host-insect and host food-plant populations to wider environmental heterogeneity. In this study it was shown aside from the influence of host-plant heterogeneity that habitat heterogeneity driven by cattle grazing affected parasitism rates. This is analogous to studies that have found at coarser spatial scales the amount of parasitism in a habitat patch to be affected by the composition or heterogeneity of the surrounding landscape (Kruess 2003; Thies *et al.* 2003). This study supports the idea that parasitism is sensitive to heterogeneity from sources beyond the immediate host or habitat patch and provides evidence of how trophic interactions may be altered by anthropogenic disturbance. Indeed a critique of this thesis is while landscape-scale environmental heterogeneity is considered in the study of soil fauna diversity, it would have been prudent given the published evidence on how landscape context influences both diversity and interactions (Steffan-Dewenter *et al.* 2002; Tscharntke *et al.* 2002b; Kruess 2003; Steffan-Dewenter 2003) to have considered influence of the landscape context of the birch woods on the diversity of different trophic guilds and parasitism rates. Indeed it would be interesting to compare the relative importance of the landscape context of the birch woods and the impact of the local disturbance to the habitat resulting from the introduction of cattle for invertebrate diversity and trophic interactions.

The finding that interactions (parasitism) are, along with species diversity, sensitive to environmental heterogeneity arising from human activities is of relevance to those interested in conservation. Biodiversity conservation has generally been traditionally focussed at the conservation of species and species diversity (Wilson 1988; Diamond 1975; Diamond & Gilpin 1982; Begon *et al.*1996). It is being increasingly recognised that interactions between species are vulnerable to the same anthropogenic habitat losses and disturbance (Kruess & Tscarntke 1994, 2002b; Vazquez & Simberloff 2003; Fortuna & Bascompte 2006; Vanbergen et al. 2006); and that interactions and food-web structure may have a more important role than diversity alone in underpinning the stable functioning of ecosystems (McCann 2000; Loreau *et al.* 2001; Dunne et al. 2002; Montoya et al. 2003; Montoya et al. 2006). This recognition implies that measures taken to conserve biodiversity should consider not only species diversity but also the diversity and connectance of interactions, if such measures are to be both stable over time and contribute to the maintenance of ecosystem functions. In practical terms this may require setting aside areas as reserves free from those anthropogenic influences (e.g. grazing Vazquez & Simberloff 2003) that are documented to erode diversity, interactions and food-web stability.

While the functional significance of the loss of invertebrate predators reported from the study of grazing in birch woods is perhaps questionable (Loreau *et al.*2001), nonetheless this finding remains of conservation significance and is supported by evidence elsewhere reporting declines in invertebrate predator densities and diversity with disturbance to habitats (Didham *et al.* 1998b; Bromham *et al.* 1999; Davies *et al.* 2000; Purtauf *et al.* 2005). Taking into consideration the indications that invertebrate diversity and trophic guild structure can be structured by landscape-scale patterns in land-use further agricultural intensification of landscapes will have negative repercussions for biodiversity conservation, in particular for species occupying the highest trophic level. A sensible conservation approach would be to maintain a habitat mosaic (at a range of spatial and temporal scales to suit a range of taxa) in the landscape (Benton *et al.* 2003), and to avoid the intrusion and impact of agriculture into semi-natural parts of that mosaic (Vazquez & Simberloff 2003; Vanbergen *et al.* 2006), in order to provide refuges for those species most sensitive to anthropogenic disturbance. These natural patches may then function as source habitats contributing to the persistence of populations as part of metapopulations (Hanski 1999) and even species in a wider metacommunity (Leibold *et al.* 2004; Mouquet *et al.* 2006).

Constraints due to limited time and finances, logistical difficulties, and the need to balance competing areas of research meant it was not always possible to take all the individual studies within the thesis to their logical conclusion. For example, experiments were not carried out to settle whether competitive interactions between worms and collembola occur, if these can scale up to produce the observed landscape level patterns in diversity, and whether disturbance can mitigate competitive exclusion between soil fauna. Observations and experiments were not carried out on the feeding behaviour and associated fitness components (e.g. fecundity) of *T. conura* and *P. elevatus* adults to support the idea expressed in Chapter 6 that the effects of cattle engineering were transmitted to these insect populations via changes to the nectar resource (e.g. Heimpel & Jervis 2005). Similarly, the impact of habitat structure on parasitism rates was explored in Chapter 7, but the indirect effect of altered rates of parasitism on plant growth and reproduction (e.g. Matsumoto et al. 2003) were not investigated. The effect of spatial heterogeneity at different spatial scales on insect diversity and trophic interactions is the overall theme of this thesis, temporal heterogeneity was not considered being deemed at the outset beyond the scope of this thesis. Nevertheless, it should be acknowledged that a temporal component to the data presented here must exist and may have introduced a bias into the diversity data presented here.. For example, the use of a snapshot method of sampling meant that diversity may have been under represented in the studies of soil and trophic guild diversity because of seasonality in insect phenology (Brown *et al.* 1992; Borges & Brown 2001) or because of insufficient time for invertebrates to locate or re-colonise new or recently disturbed habitat patches (e.g. tilled fields) in agricultural mosaics (Benton 2003; Bardgett 2005). The timing of agricultural management was not quantified, for example, the timing of cattle grazing and its effect upon insect functional group diversity was not considered within this thesis – such an approach may reveal if the observed changes to the insect guilds persisted over time and if susceptibility to this disturbance varied over time.

It would be desirable to build on the work in this thesis to explore further the disturbing impact of anthropogenic grazing in birch woods on other species interactions (other host-parasitoid interactions, insect-plant mutualisms), and whether the effect on trophic guild structure in the woodland understorey extends below-ground to the soil invertebrate assemblages (recent preliminary data indicate that grazed woods support greater overall nematode densities, but a lower density of predatory nematodes). Pollination services are a vital ecosystem service provided to agriculture, and given the positive ramifications of this disturbance for the studied antagonistic interaction it would be interesting to discover if the elevated plant diversity leads to an increase in pollinator diversity, and in turn the parasitoids of pollinators. Plant visitation webs (Gibson *et al.* 2006) could be constructed to assess pollinator assemblage structure and collections of pollinator hosts (*Bombus* spp.) from field sites would reveal levels of parasitism. Through a combination of field observation and experimental manipulations (grazing exclosures, nutrient additions), and experimental microcosms it should be possible to disentangle the relative contribution of plant diversity, vegetation structural heterogeneity and the quality and amount of resources (e.g. litter) to the diversity and community structure of the soil food-web (Hansen & Coleman 1998; Hasegawa 2002; Wardle *et al.* 2003; Wardle *et al.* 2004). This system of disturbed and undisturbed birch woods represents an opportunity to assess how an anthropogenic global change (land-use, invasions, climate) can influence diversity, population and food-web stability. Moreover, it is both a natural experiment in the real world and of a spatial scale amenable to direct, experimental manipulation to elucidate specific mechanisms and feedbacks.

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APPENDIX I. Species abundances in the 6 LUUs, data are pooled catches from two years (2001, 2002) per LUU

Species	Authority	LUU1	LUU2	LUU3	LUU4	LUU5	LUU6
Agonum assimile	(Paykull, 1790)	0	0	0	5	0	12
Agonum muelleri	Herbst, 1784	0	0	0	251	1232	857
Anchomenus dorsalis	(Pontoppidan, 1763)	0	0	0	19	954	931
Amara aenea	(Degeer, 1774)	0	0	12	20	8	1
Amara apricaria	(Paykull, 1790)	0	0	0	0	13	2
Amara aulica	(Panzer, 1797)	0	0	6	2	4	4
Amara bifrons	(Gyllenhal, 1810)	0	0	0	1	3	5
Amara communis	(Panzer, 1797)	0	0	9	5	0	0
Amara eurynota	(Panzer, 1797)	0	0	0	1	2	0
Amara familiaris	(Duftschmid, 1812)	0	0	3	8	15	1
Amara fulva	(Müller, 1776)	0	0	0	0	9	0
Amara lunicollis	Schiødte, 1837	0	0	1	24	51	0
Amara plebeja	(Gyllenhal, 1810)	0	0	0	19	289	152
Bembidion bruxellense	Wesmael, 1835	0	0	0	0	3	30
Bembidion guttula	(F., 1792)	0	0	0	0	134	112
Bembidion lampros	(Herbst, 1784)	0	0	1	37	355	37
Bembidion mannerheimii	Sahlberg, 1827	0	0	1	18	74	10
Bembidion tetracolum	Say, 1823	0	0	0	0	1876	626
Bradycellus harpalinus	(Audinet-Serville, 1821)	0	1	0	0	0	0
Calathus fuscipes	(Goeze, 1777)	0	3	215	334	383	295
Calathus melanocephalus	(L., 1758)	0	0	17	37	68	313
Calathus micropterus	(Duftschmid, 1812)	81	1252	136	18	2	12
Calathus rotundicollis	Dejean, 1828	0	22	215	36	3	2
Carabus glabratus	Paykull, 1790	367	141	30	0	0	1
Carabus granulatus	L., 1758	3	0	2	0	0	0
Carabus nemoralis	Müller, 1764	0	3	4	8	1	3
Carabus problematicus	Herbst, 1786	17	1204	361	44	0	11
Carabus violaceus	L., 1758	247	259	119	85	0	0
Cicindela campestris	L., 1758	1	0	0	0	0	0
Clivina fossor	(L., 1758)	0	0	8	17	253	256
Cychrus caraboides	(L., 1758)	81	91	24	6	1	2
Dromius agilis	(F., 1787)	0	0	1	0	0	0
Elaphrus cupreus	Duftschmid, 1812	0	0	0	0	2	0
Harpalus affinis	(Schrank, 1781)	0	0	0	0	9	0
Leistus fulvibarbis	Dejean, 1826	0	0	0	1	0	2
Leistus spinibarbis	(F., 1775)	0	0	2	1	0	0
Leistus terminatus	(Hellwig in Panzer, 1793)	11	290	50	25	8	11
Loricera pilicornis	(F., 1775)	5	67	138	269	450	369
Nebria brevicollis	(F., 1792)	1	18	173	1211	3287	3900
Nebria rufescens	Strom, 1768 (Sch., 1806)	0	0	3	5	3	9
Nebria salina	Fair. & Labou., 1854	0	185	14	0	2	1
Notiophilus aquaticus	(L., 1758)	1	0	0	0	3	0
Notiophilus biguttatus	(F., 1779)	10	22	116	37	181	39
Patrobus atrorufus	(Ström, 1768)	0	0	0	62	8	141
Pterostichus adstrictus	Eschscholtz, 1823	1	161	16	2	0	0
Pterostichus diligens	(Sturm, 1824)	2	0	0	0	0	0
Pterostichus madidus	(F., 1775)	0	147	4103	416	1054	465
Pterostichus melanarius	(Illiger, 1798)	0	1	1	261	206	1275
Pterostichus niger	(Schaller, 1783)	5	0	303	119	508	561
Pterostichus nigrita	(Paykull, 1790)	6	11	15	61	181	19
Pt.oblongopunctatus	(F., 1787)	341	458	96	110	0	2
Pterostichus strenuus	(Panzer, 1797)	3	1	47	142	83	95
Stomis pumicatus	(Panzer, 1796)	0	0	0	0	2	0
Synuchus vivalis	(Illiger, 1798)	0	0	5	0	17	13
Trechus micros	(Herbst, 1784)	0	0	0	0	0	7
Trechus quadristriatus	(Schrank, 1781)	18	109	28	70	74	337
Trichocellus cognatus	(Gyllenhal, 1827)	0	0	0	1	0	0
Trichocellus placidus	(Gyllenhal, 1827)	0	0	0	0	1	0

APPENDIX II. Intercorrelation between 11 habitat variables measured in 10 grazed and 10 ungrazed birch woodlands. Values are Pearsons correlation coefficients (P = 0.06†, P<0.05*, P<0.01**, P<0.001***). Variables are the percentage cover of bare and disturbed soil, forbs, grasses and bryophytes; the tree canopy density (%), height of the sward (mm), spatial variability in sward height (CV^2), the number of vascular plant species (Plant *S*), forb species (Forb *S*) and grass species (Grass *S*) and the area (ha) of the woodland.

Habitat variables	Sward	Sward CV	Bare soil	Forb	Grass	Bryophyta	Plant *S*	Forb *S*	Grass *S*	Area
Canopy	0.05	0.04	-0.18	-0.20	-0.13	**0.44***	**-0.59****	**-0.41†**	**-0.50***	-0.21
Sward		0.26	**-0.48***	**-0.49***	0.31	-0.10	-0.36	**-0.54****	0.16	-0.03
Sward CV			0.18	0.24	-0.23	-0.28	0.016	0.15	-0.11	-0.05
Bare soil				**0.47***	-0.09	-0.38	**0.47***	**0.52***	0.27	-0.18
Forb					-0.16	**-0.44***	**0.43†**	**0.69****	0.13	-0.19
Grass						**-0.58****	-0.20	-0.30	**0.42†**	0.18
Bryophyta							-0.33	-0.39	**-0.52***	-0.08
Plant *S*								**0.86*****	**0.56****	0.25
ForbSR									0.27	0.12
GrassSR										0.10

APPENDIX III. Invertebrate species sampled from 10 grazed and 10 ungrazed birch woodlands

Species	Taxa	Guild
Anthocoris nemorum L.	Heteroptera	predator
Linypha triangularis (Clerck)	Araneae	predator
Philaenus spumarius L.	Auchenorrhyncha	herbivore
Mecomma ambulans Fallen	Heteroptera	omnivore
Enoplognatha ovata (Clerck)	Araneae	predator
Lygocoris pabulinus L.	Heteroptera	herbivore
Meta mengei (Blackwall)	Araneae	predator
Javesella spp.	Auchenorrhyncha	herbivore
Notus flavipennis Zetterstedt	Auchenorrhyncha	herbivore
Tetragnatha montana Simon	Araneae	predator
Monalocoris filicis L.	Heteroptera	herbivore
Lygocoris contaminatus Fallen	Heteroptera	herbivore
Meligethes aeneus (Fabricius)	Coleoptera	herbivore
Jassargus distinguendus (Flor)	Auchenorrhyncha	herbivore
Bryocoris pteridis Fallen	Heteroptera	herbivore
Eupteryx vittata L.	Auchenorrhyncha	herbivore
Neriene peltata (Wider)	Araneae	predator
Betulapion simile (Kirby, 1811)	Coleoptera	herbivore
Ceratapion carduorum (Kirby, 1808)	Coleoptera	herbivore
Cyphon sp.	Coleoptera	herbivore
Epuraea sp.	Coleoptera	herbivore
Thamnotettix confinis Zetterstedt	Auchenorrhyncha	herbivore
Plagiognathus arbustorum Fabricius	Heteroptera	omnivore
Anthophagus caraboides (Linnaeus, 1758)	Coleoptera	predator
Stenus picipes Stephens, 1833	Coleoptera	predator
Otiorhynchus scaber (Linnaeus, 1758)	Coleoptera	herbivore
Perapion curtirostre (Germar, 1817)	Coleoptera	herbivore
Pachytomella parallela Meyer-Dur	Heteroptera	herbivore
Cicadella viridis L.	Auchenorrhyncha	herbivore
Eupteryx aurata L.	Auchenorrhyncha	herbivore
Malthodes flavoguttatus Kiesenwetter	Coleoptera	omnivore
Theridion varians Haha	Araneae	predator
Strophosoma melanogrammum (Forster, 1771)	Coleoptera	herbivore
Crepidodera ferruginea (Scopoli, 1763)	Coleoptera	herbivore
Polydrusus undatus (Fabricius, 1781)	Coleoptera	herbivore
Kleidocerys resedae Panzer	Heteroptera	herbivore
Lygocoris sp.	Heteroptera	herbivore
Psallus sp.	Heteroptera	herbivore
Stenodema laevigatum L.	Heteroptera	herbivore
Evancanthus interruptus L.	Auchenorrhyncha	herbivore
Neophilaenus lineatus L.	Auchenorrhyncha	herbivore
Rhytidodus decimusquatus Schrank	Auchenorrhyncha	herbivore
Cercyon lateralis (Marsham, 1802)	Coleoptera	omnivore
Malthodes guttifer Kiesenwetter	Coleoptera	omnivore
Malthodes mysticus Kiesenwetter	Coleoptera	omnivore
Rhagonycha femoralis (Brulle)	Coleoptera	omnivore
Pocadicnemis pamila (Blackwall)	Araneae	predator
Aleocharinae sp.	Coleoptera	predator
Stenus aceris Stephens, 1833	Coleoptera	predator
Bathyphantes gracilis (Blackwall)	Araneae	predator
Cyclosa conica (Pallas)	Araneae	predator
Erigone dentipalpis (Wider)	Araneae	predator
Lepthyphantes tenebricola (Wider)	Araneae	predator
Lepthyphantes tenuis (Blkackwall)	Araneae	predator
Nabis flavomarginatus Scholtz	Heteroptera	predator
Saldula scotica Curtis	Heteroptera	predator

APPENDIX IV. Paper submitted to Journal of Animal Ecology April 2006.

Parasitoid species identity determines the impact of bottom-up effects on parasitism rates of a specialist insect herbivore

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Summary

While there is considerable theoretical interest into the role of habitat heterogeneity in stabilising host–parasitoid systems, there remains a paucity of empirical studies within natural systems. We investigate the responses of a suite of parasitoid species attacking a single host to heterogeneity in host insect abundance, host-plant canopy patch area and host-plant characteristics (size and location).

Within a birch dominated woodland 88 *Fagus sylvatica* trees were sampled for the leaf mines of the specialist beetle herbivore *Rhynchaenus fagi*. Host *F. sylvatica* trees occurred in patches throughout the birch woodland varying in size from isolated individuals to clumps of up to nine trees. Leaf-mine abundance and percentage parasitism by hymenopteran parasitoids was sampled from each tree.

Herbivore mine abundance was greatest where trees were located on the edge, compared with the interior, of the birch woodland. Parasitism rates of *R. fagi* showed independent, direct, and inverse responses to the density of leaf mines depending on parasitoid species identity.

The two smallest parasitoid species, *Pnigalio longulus* and *Chrysocharis nephereus*, were respectively positively and negatively correlated with the canopy area of host-plant patches, and positively, but weakly, correlated with tree trunk diameter. The largest parasitoid species, *Colastes braconius*, was unaffected by canopy area.

Host-plant position (edge v. interior) modified *P. longulus* parasitism by interacting with host-insect density. Parasitism was density-independent within the woodland interior, and inversely density-dependent where trees were situated at the woodland edge.

The persistence of species within this multi-parasitoid assemblage is likely to be shaped by heterogeneity in both host insect abundance and the distribution of host-plants. The relative importance, however, of the different sources of environmental heterogeneity depends on parasitoid species identity. Only for one (*C. braconius*) of three parasitoids was the interaction with the host insect species stable under the $CV^2 > 1$ rule.

Keywords: bottom-up, $CV^2 > 1$, parasitism, spatial heterogeneity, density-dependence.

Introduction

The complexity of interactions in multi-parasitoid food webs are dependent on the mechanisms of coexistence allowing parasitoids to utilise either single or multiple hosts (Bonsall & Hassell, 1997; Amarasekare, 2000; Hassell, 2000a). The persistence of multiple species assemblages may be promoted by a number of potential, although not always mutually exclusive, mechanisms (Bonsall *et al.*, 2004). These include behavioural processes resulting in aggregation and segregation of individuals (Sevenster & Van Alphen, 1993; Woodcock, Watt & Leather, 2002), niche partitioning of resources (Naeem & Hawkins, 1994; Wieber *et al.*, 1995), dispersal ability (Kareiva, 1987; Amarasekare, 2000) and life history trade offs (Bonsall, Hassell & Asefa, 2002).

Understanding the processes that drive regional dynamics of predator-prey or host-parasitoid interactions requires an understanding of the factors that determine both rates of colonization and local extinction (Hanski, 1999; Cronin, 2004). In host-parasitoid systems variation in parasitism rates are known to be affected by the influence of habitat complexity on parasitoid dispersal rates and the probability of host-patch colonization (Kareiva, 1987; Cronin & Strong, 1999). The mechanism of host location by parasitoids - by chemical and physical cues (reviewed in Quicke, 1997) - will be influenced by the complexity of the habitat within which they persist. As habitat complexity is reduced, the probability of host location by parasitoids becomes more likely, relative to what would be expected from more spatially structured or complex landscapes (Gols *et al.*, 2005). Habitat heterogeneity will, therefore, introduce variation in parasitism rates among hosts, stabilizing the host-parasitoid relationship (Huffaker, 1958; Hassell, 2000b). In addition to habitat heterogeneity, the presence of refuges and aggregation are also key mechanisms promoting stability in tightly coupled host–parasitoid associations (Huffaker, 1958; Hassell & May, 1973). Furthermore, host location within patchy environments will be influenced by secondary factors including habitat location, the spatial positioning of host species within that habitat and individual host quality (Vinson & Iwantsch, 1980a, 1980b).

The influence of heterogeneity at a landscape scale will not influence all species in the same manner, as individual species within a parasitoid assemblage will have different dispersal powers and strategies for host location and colonisation (Kareiva, 1987; Hanski, 1999). It is this variation in dispersal abilities and its influence on patch colonisation within a heterogeneous landscape, which will influence both the persistence of individual species and the assemblage structure of host-parasitoid associations (Jones, Godfray & Hassell, 1996; Hassell, 2000b; Van Nouhuys & Hanski, 2002).

In addition to the factors influencing dispersal and colonisation, considerable variation is likely between parasitoid and host insects in the factors driving local population turnover (Van Nouhuys *et al.*, 2002; Cronin, 2004). It is known that tertiary trophic levels are often more susceptible to habitat fragmentation than secondary consumers (Kareiva, 1987; Tscharntke & Brandl, 2004; Elzinga *et al.*, 2005), and levels of parasitism may be reduced in isolated habitat patches (Roland & Taylor, 1997; Doak, 2000; Kruess & Tscharntke, 2000; Cronin, 2003; Elzinga *et al.*, 2005). Once established in a given patch the persistence of individual species within a habitat matrix will be dependent on a variety of environmental and demographic factors, including inbreeding depression (Hanski & Heino, 2003), weather (Solbreck, 1991), changes in the rates of parasitism (Eber, 2001; Cobbold *et al.*, 2005) and host plant species (Van Nouhuys *et al.*, 2002). Patch size itself will also contribute to the potential for local extinction, with smaller populations generally being at greater risk (Pimm, Jones & Diamond, 1988; Cronin, 2003).

To determine mechanisms underpinning host-parasitoid interactions in a naturally patchy habitat we investigated the responses of a suite of parasitoids attacking a single host to spatial heterogeneity in the distribution of host insects and the host plant resources. We sampled populations of the beech leaf-miner *Rhynchaenus fagi* L. (Curculionidae, Coleoptera) and associated parasitoids on *Fagus sylvatica* trees (Beech) distributed in discrete patches within a predominantly birch woodland. This was done to test the following null hypotheses:

$H0_1$: There is no numerical response shown by parasitoids host insect density.
$H0_2$: There is no numerical response shown by parasitoids to the patch size of the host plant *F. sylvatica.*
$H0_3$: There is no numerical response shown by parasitoids to individual attributes of host plant trees.

$H0_4$: Where numerical responses to either host insect density or host plant patch area were found, these were unaffected by the spatial location of the *F. sylvatica* trees in relation to the woodland edge or interior.
$H0_5$: There is no evidence of interactions between the parasitoid species in terms of their percentage parasitism of the *R. fagi* host.

Materials and methods

STUDY SITE

The study site was a single deciduous woodland stand in Banchory, Aberdeenshire, Scotland (57°04'N, 2°32'W). The woodland was dominated (>80% of the total area) by two species of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.), with occasional patches of Scots pine (*Pinus sylvestris* L.). Grasses, particularly *Holcus* spp., *Festuca* spp. and *Deschampsia* spp. together with patches of bracken *Pteridium aquilinum* (L.) dominated the understorey, and large patches of moss and bare ground were also present. Interspersed into this birch woodland were 88 *Fagus sylvatica* trees, the host plant of *R. fagi*. The woodland covered an area of 28 hectares and was surrounded by either Scots pine dominated plantation or areas of the plantation that had been clear felled no less than 7 years prior to sampling in 2005. *F. sylvatica* trees with a trunk diameter at breast height (DBH) of less than 5 cm were ignored.

TRI-TROPHIC SYSTEM

Rhynchaenus fagi is a univoltine leaf-mining weevil which feeds as larvae exclusively on *F. sylvatica* trees, although adults will feed on a variety of plants (Bale & Luff, 1978). Adult weevils overwinter primarily within leaf litter (Bale, 1979, 1984) until mid-March, when the majority of adults will migrate to *F. sylvatica* trees just prior to bud burst. Some individuals will, however, remain within leaf litter until after this time (Nielsen, 1970, 1974). Eggs are laid in the leaf mid-rib from where a linear blotch-mine develops within which the larvae feed on both the palisade and spongy parenchyma (Nielsen, 1966). From oviposition to emergence of the weevil takes approximately 30-35 days, with adults appearing towards the end of June (Bale *et al.*, 1978). *Rhynchaenus fagi* has a relatively diverse fauna of hymenopteran parasitoids, with Askew & Shaw (1974) rearing ten chalcid species within the UK from the mines of this weevil. Braconid parasitoids have also been reared from this weevil (Day & Watt, 1989; Rott & Godfray, 2000).

HOST-PLANT VARIABLES

For each of the 88 *F. sylvatica* trees present within the woodland the following measurements were taken. Tree trunk diameter at breast height (DBH) and the canopy diameter (mean of two measures per tree) were measured. The individual canopy diameter of each tree was then used to calculate the canopy area of *F. sylvatica* habitat patches (PATCH) represented by both individual trees and clumps of trees whose canopies overlapped, and therefore represented a continuous patch of *F. sylvatica* canopy to dispersing *R. fagi*. As some *F. sylvatica* trees occurred on the edge of the woodland adjoining areas of clear-cut coniferous plantation forestry, trees were categorised as being either woodland edge or interior trees (EDGE).

INSECT SAMPLING

All sampling occurred in June 2005 towards the end of *R. fagi* larval development. A branch was excised from both the North and South aspect of each of the 88 *F. sylvatica* trees at a height of between 1.5 and 4.0 m off the ground. Although only 11% of the leaves of a *F. sylvatica* tree are found in this lower canopy strata, previous work has shown that 75-85% of these received some form of phytophagous invertebrate damage, representing approximately 35 % of the total phytophage damage to an individual tree (Phillipson & Thompson, 1980). 50 leaves were randomly picked from each branch giving a total of 100 leaves sampled per tree. From these samples of leaves the proportion of leaves from an individual tree mined by *R. fagi* was calculated.

A sub-sample of ten randomly chosen leaves, each containing a single *R. Fagi* leaf-mine, were removed from both the North and South aspect of each tree (20 leaves per tree, 1760 leaves in total). Each leaf-mine was examined to ensure that a living *R. fagi* larva was present. The sub-samples from each tree (n = 10 x 2) were placed into Organza™ covered plastic pots in an insectary adjacent to the woodland (which maintained a similar temperature regime to that of the woodland). Every two days the leaves were checked and emerging adult *R. fagi* and parasitoids were removed and transferred to 70 % IMS. Inspection of the mines continued for a 4-week period after the last emergence of either the host or parasitoid. All parasitoids were subsequently identified to species and compared to reference material at the Hope Entomological Collection, Oxford.

STATISTICAL ANALYSIS

Although leaf mines were collected from branches on both the North and South sides of trees these values were summed so that either the number of mines or parasitoid emergence per tree represented the sample unit. Percentage herbivory of *F. sylvatica* by *R. fagi* (leaf mine abundance per 100 leaves) and percentage parasitism of *R. fagi* (parasitoid count per 20 leaves) were modelled with generalised linear mixed models (GLMM) with Binomial error distribution and Logit link (SAS Institute, 1999). The influence of four fixed effects on percentage herbivory by *R. fagi* were considered: 1) the position of *F. sylvatica* trees within the woodland interior or at the woodland edge (EDGE); 2) the diameter at breast height of individual *F. sylvatica* tree trunks (DBH); 3) the canopy area of *R. fagi* habitat patches (isolated *F. sylvatica* individuals or clumps of *F. sylvatica* trees with overlapping canopies) (PATCH). Also considered was the two–way interaction between EDGE*DBH and EDGE*PATCH. In addition to the main effects and interactions described above, percentage parasitism of *R. fagi* by each parasitoid species was also correlated to the main effect of host insect density (MINES) and the interaction of this with tree position (EDGE*MINE). It was not possible to directly test for interspecific competition or interference between different parasitoid species because only parasitoid emergence was measured. Instead percentage parasitism by each species was correlated (GLMM, Binomial error and Logit link) to the count of the other parasitoid species emerging from the leaf-mines.

Solution of fixed explanatory (EDGE, PATCH, DBH, MINES) and random (categories: 'Tree identity' and 'Patch identity') effects was estimated by residual maximum likelihood (REML). Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell *et al.*, 1996; Schabenberger & Pierce, 2002). Model simplification was by step-wise elimination of the least significant term until the most parsimonious model was found; where a significant interaction occurred its component parameters were not deleted, even if individually non-significant. F-ratios of main effects and interactions using sequential sums of squares (SAS Type 3 tests) are reported.

Results

A total of 88 *F. sylvatica* trees were sampled within the birch woodland of which 15 trees were considered to be present on the edge of the site. Sixteen patches containing two or more *F. sylvatica* trees were present within the birch woodland, with the largest patch of nine trees covering an area of 1265.6 m^2. From the 1,760 leaf-mines returned to the insectary 10 % yielded *R. fagi* adults (n = 176) while 31 % of mines were parasitized (551 parasitoids) by one of four species of hymenopteran parasitoid, under the assumption of solitary larvae (Askew *et al.*, 1974). This left 59 % of the mortality of the insectary reared *R. fagi* unexplained. Of the four parasitoids, three species represented 95 % of the total parasitoid abundance: *Pnigalio longulus* (Zett.) (Eulophidae) (n = 225 individuals); *Chrysocharis nephereus* (Walker) (Eulophidae) (n = 182); and *Colastes braconius* Haliday (Braconidae) (n = 129). The remaining parasitoid (*Pnigalio soemius* (Walker)) (Eulophidae) was represented by only 25 individuals, and due to this low representation within the samples it was excluded from the subsequent analyses.

INFLUENCE OF HOST-PLANT HETEROGENEITY ON HERBIVORY & PARASITISM

The amount of herbivory by *R. fagi* was affected by the position of the host tree within the woodland (EDGE): percentage herbivory was significantly greater at the woodland edge ($\bar{x}$ = 0.78 s = 0.23) compared to trees in the woodland interior ($\bar{x}$ = 0.45 s = 0.31) (Table 1). Herbivory in *R. fagi* was not significantly affected by any of the other measured host-tree parameters (Table 1). For all three parasitoids, percentage parasitism of *R. fagi* was not directly affected by whether the host tree was located at either the woodland edge or interior (Table 1). The host tree size (trunk diameter) was a significant and marginally significant positive predictor of the proportion of mines parasitized by *C. nephereus* and *P. longulus* respectively (Table 1, Fig.1a-b). The rate of *C. braconius* parasitism was affected by the interaction between host-plant trunk diameter and tree position. There was a positive relationship between trunk diameter and percent parasitism when the trees were located at the woodland edge, while this relationship disapeared when the trees considered were found in the woodland interior (Table 1, Fig.1c). The canopy area of the *F. sylvatica* patches – the host insect resource - was a highly significant predictor of percentage parasitism for two of the three parasitoid species: *P. longulus* was positively and *C. nephereus* negatively correlated to patch canopy area (Table 1, Fig.2), while *C. braconius* was not affected (Table 1).

HOST-PARASITOID INTERACTIONS

Percentage parasitism by *C. braconius* was significantly and positively correlated with host-insect mine density, while parasitism by *C. nephereus* was independent of host-insect mine density (Table 1, Fig. 3a). *Pingalio longulus* parasitism was affected by a significant interaction between host insect mine density and *F. sylvatica* tree position (MINE*EDGE, Table 1, Fig. 3b). Where trees were located in the woodland interior the slope of the response to host- insect mine density did not differ significantly from zero (b = -0.02 t = -0.21 p =0.83). However, where trees were located at the woodland edge there was a highly significant and inverse relationship between *P. longulus* parasitism and host mine density (b = -1.10, t = -3.31 p = 0.001). The percentage parasitism of each of the three parasitoid species was unaffected by the density of the other parasitoid species attacking *R. fagi*, therefore there was no evidence of direct interactions between the parasitoid species (Table 2).

The overall stability of the host-parasitoid interaction was tested using the $CV^2>1$ rule, which states that the interaction between the host and parasitoid will be stable if the coefficient of variation of searching parasitoids per patch (CV^2) is greater than 1 (Pacala, Hassell & May, 1990; Hassell *et al.*, 1991; Pacala & Hassell, 1991). The $CV^2>1$ rule was tested at the level of individual trees (n = 88) and for patches of trees (43 patches of 1 or more trees). In all cases the number of parasitoids per patch was weighted for the number of potential hosts, which was considered to be the number of mines per tree or patch. The values of CV^2 for *C. braconius* (tree: 1.82, patch: 1.18), *P. longulus* (tree: 0.51, patch: 0.39) and *C. nephereus* (tree: 0.97, patch: 0.41) revealed that the host-parasitoid association was stable only for the largest species, the braconid *C. braconius*.

Discussion

This study provides evidence for bottom up forces influencing rates of parasitism within the *R. fagi* host – multi-parasitoid system, as a function of hymenopteran parasitoid species identity. While no evidence for direct interactions between the hymenopteran parasitoids of the leaf mining weevil *R. fagi* were found (hypothesis $H0_5$), variation in the rates of parasitism between these species were found in their response to host insect density, host plant patch area, to the physical characteristics of individual trees and to the spatial location of the host plants. Respectively, this resulted in the rejection of hypothesis $H0_1 – H0_4$.

HOST INSECT DENSITY

At the spatial scale of individual trees, host insect density was a significant predictor of parasitism rates for both the braconid *C. braconius* and the chalcid *P. longulus*. The direction of this response to host insect density was not consistent in these two species. *Colastes braconius* parasitism was directly density-dependent, and although not explicit demonstrated in our data such aggregation of parasitoids to patches of high host density has been shown to contribute to temporal stability in other host–

parasitoid interactions (e.g. Hassell *et al.*, 1973; Hassell & May, 1974). In addition to being the only parasitoid to show such direct density dependence, *C. braconius* was alone in being spatially stable according to the $CV^2 > 1$ criterion (Pacala *et al.*, 1990; Hassell *et al.*, 1991). Density dependence in parasitism rates has been suggested to be caused by species specific searching behaviour resulting in increased attraction to, and residency time in, areas of high host density (Hassell, 1978; Stiling, 1987; Doak, 2000). Such responses to increased host density are predicted under optimal foraging theory (Cook & Hubbard, 1977; Hubbard & Cook, 1978) and result in the creation of probabilistic refuges within which host persistence is more likely (Hassell *et al.*, 1991).

In contrast to the density-dependent response of *C. braconius*, parasitism by *C. nephereus* was independent of host –insect density, while the response of *P. longulus* to host density was modified by spatial heterogeneity in the food resource of the host insect. For host trees present in the woodland interior parasitism of *R. fagi* by *P. longulus* was density independent, whereas on host trees located on the woodland edge *R. fagi* experienced inverse density-dependent parasitism. Patterns of inverse density-dependence may reflect longer handling times during host location and oviposition or interference among parasitoids (Waage, 1983; Visser, Jones & Driessen, 1999) reducing parasitoid efficiency in exploiting high density patches (Lessells, 1985; Stiling, 1987; Taylor, 1993). Alternatively, inverse density dependence may arise through 'risk spreading behaviour' resulting in an absence of parasitoid aggregation to areas of high host density (Strong, Antolin & Rathbun, 1990). From our data, however, we have no evidence of direct interactions (competition, hyperparasitism) between the parasitoid species. Potentially the location of the tree at the woodland edge may constitute a refuge from parasitism if aversion to differences in microclimate impact on the ability of *P. longulus* to use the host's habitat as cue to locate the host insect. Overall in this study, the different parasitoid responses to host density broadly reflect the suggestion by Stiling (1987) that direct and inverse dependence occur in 25 % and 23 % of host parasitoid interactions respectively.

HABITAT PATCH AREA

The increased sensitivity to habitat fragmentation or patchiness within tertiary trophic levels relative to secondary consumers has been seen from both a range of systems and spatial scales (Kruess & Tscharntke, 1994; Didham *et al.*, 1998; Davies, Margules & Lawrence, 2000; Thies, Steffan-Dewenter & Tscharntke, 2003). A reduction in habitat patch area or increases in the degree of isolation have been shown to result in reduced rates of parasitism in a number of cases (Roland *et al.*, 1997; Doak, 2000; Cronin, 2003, 2004; Elzinga *et al.*, 2005). In this study canopy patch area influenced parasitism rates positively for *P. longulus* and negatively for *C. nephereus*, while *C. braconius* was insensitive to the area of the host plant patches. This finding confirms that parasitism rates or parasitoid behaviour can be influenced by not only host abundance, but also by heterogeneity in host resources (Cappuccino, 1992; Doak, 2000). This is potentially the result of searching parasitoids using host resources as cues to commence searching for the more cryptic hosts (Cappuccino, 1992).

Differential responses to spatial heterogeneity in host resources are likely to stem from intrinsic differences between the parasitoids in terms of their ability to colonise, disperse and locate new hosts (Kareiva, 1987; Hanski, 1999; Van Nouhuys *et al.*, 2002). The spatial scale at which different species perceive habitat patchiness may relate to differences in body size, a surrogate of dispersal ability (Roland *et al.*, 1997). Differences in relative body size between the parasitoid species of this study could explain the differential response of the parasitoids to the canopy patch area. *Colastes braconius* was at least 2-3 times larger than the other parasitoid species, and thus it is assumed possessed greater powers of dispersal, making it less sensitive to the variable area of the habitat patches. The smaller species *P. longulus* and *C. nephereus*, by contrast, are sensitive to the area of the habitat patch. There was no effect of patch area on herbivore density, thus parasitoids were not simply tracking host numbers in larger habitat patches. While not explicit from our available data, the implication is that the three parasitoid species attacking *R. fagi* perceive the spatial patchiness of the habitat differently, most likely as a consequence of differences in dispersal ability.

INDIVIDUAL CHARACTERISITCS OF THE HOST PLANTS

Parasitism rates by the three species of parasitoid were influenced by variation in tree trunk diameter, therefore between tree heterogeneity independent of host insect density influenced parasitism rates for *R. fagi*. Tree trunk diameter is an indirect index of tree age, health and size (Thomas, 2000), although which of these influenced rates of parasitism is unclear. Spatial heterogeneity in the host tree distribution interacted with trunk diameter to influence *C. braconius* parasitism, which was positively correlated with tree trunk diameter at the woodland edge, while negatively correlated within the woodland interior. This change in the response to tree trunk diameter between the edge and the interior may be due to differences in both ambient temperature, timing of bud burst (and so host availability) and leaf nutritional quality in these two areas. There is evidence for *R. fagi* that selection for individual trees does occur (Bale, 1984). This indicates that the importance of individual trees as resources for larval development is both variable and that this variation is detectable by the miner. It is likely, therefore, that variation in the quality of either the host plant or the *R. fagi* host is also detectable by the parasitoids (Quicke, 1997).

CONCLUSIONS

A large proportion of the mortality of *R. fagi* (58.4 %) was from unidentified sources. These unexplained mortality factors may contribute to the population regulation of *R. fagi*, as there is evidence that such sources of unidentified mortality may act in a density dependent manner for *R. fagi* (Day *et al.*, 1989). One of the major likely causes of unidentified mortality for *R. fagi* is phenological asynchrony with the host-plant inhibiting mine development (Nielsen, 1966, 1968; Bale, 1979; Day *et al.*, 1989). Allowing for these other sources of mortality, parasitism by hymenopterans remained an important component of *R. fagi* mortality. The responses of the three parasitoid species to bottom-up heterogeneity was idiosyncratic particularly with respect to host insect density, habitat patch area and the spatial location of the host-plant. Evidence for bottom-up forces acting to stabilize the host-parasitoid interactions (based on the $CV^2>1$) was, however, limited to only one of the three species (*C. braconius*). The $CV^2>1$ criterion may, however, be insufficient in some cases to accurately assess the stability of host-parasitoid interactions (Hochberg, Elmes & Clarke, 1996; Gross & Ives, 1999), therefore some of the other host-parasitoid interactions may have been more stable than indicated. There was also correlative evidence for 'edge effects' modifying two of the three host-parasitoid interactions to produce contrasting patterns of parasitism depending on the location of the hosts' food-plant either at the woodland edge or interior. A finding demonstrating how a functional response between host density and parasitism rates may be affected by fragmentation altering the habitat edge: interior ratio. This heterogeneity in parasitism indicates the complex and variable nature of responses of parasitoids to spatial habitat structure and host density.

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Table 1. The effect of *F. sylvatica* tree position (EDGE), host insect (*R. fagi*) density (MINES), *F. sylvatica* trunk diameter (DBH), *F. sylvatica* patch area (PATCH) on percentage *R. fagi* herbivory and percentage parasitism of *R. fagi* by three parasitoid species. Results of Type 1 F-tests from GLMM with binomial error distribution and Logit link. Model simplification was by step-wise removal of the least significant term, with interactions dropped before main effects.

	R. fagi		*C. braconius*		*P. longulus*		*C. nephereus*	
	(% herbivory)		***(% parasitism)***		***(% parasitism)***		***(% parasitism)***	
	F $_{(df)}$	*P*	**F** $_{(df)}$	*P*	**F** $_{(df)}$	*P*	**F** $_{(df)}$	*P*
EDGE	**13.40** $_{(1, 5)}$	**0.01**	0.28 $_{(1, 32)}$	0.60	2.90 $_{(1, 13)}$	0.11	2.31 $_{(1, 20)}$	0.14
MINES	-	-	**8.25** $_{(1, 82)}$	**0.005**	0.22 $_{(1, 81)}$	0.64	0.28 $_{(1, 69)}$	0.60
DBH	0.08 $_{(1, 58)}$	0.78	0.02 $_{(1, 82)}$	0.88	**4.08** $_{(1, 80)}$	**0.05**	**5.47** $_{(1, 48)}$	**0.02**
PATCH	1.24 $_{(1, 6)}$	0.31	0.01 $_{(1, 16)}$	0.93	**22.11** $_{(1, 11)}$	**0.0006**	**25.56** $_{(1, 36)}$	**<.0001**
MINES * EDGE	-	-	1.03 $_{(1, 76)}$	0.31	**9.98** $_{(1, 77)}$	**0.002**	0.69 $_{(1, 48)}$	0.41
PATCH * EDGE	0.00 $_{(1, 8)}$	1.00	2.52 $_{(1, 19)}$	0.13	0.02 $_{(1, 13)}$	0.90	0.01 $_{(1, 13)}$	0.93
DBH* EDGE	0.01 $_{(1, 77)}$	0.92	**4.10** $_{(1, 82)}$	**0.05**	2.22 $_{(1, 80)}$	0.14	0.52 $_{(1, 81)}$	0.47

Table 2. The influence of inter-specific parasitoid density on percentage parasitism of *R. fagi* by three parasitoid species. Results of Type 1 F-tests from GLMM with binomial error distribution and Logit link.

	C. braconius		*P. longulus*		*C. nephereus*	
	(% parasitism)		***(% parasitism)***		***(% parasitism)***	
	F $_{(df)}$	*P*	**F** $_{(df)}$	*P*	**F** $_{(df)}$	*P*
C. braconius (n)	-	-	0.42 $_{(1, 85)}$	0.52	0.36 $_{(1, 75)}$	0.55
P. longulus (n)	0.70 $_{(1, 85)}$	0.41	-	-	0.15 $_{(1, 85)}$	0.70
C. nephereus (n)	0.32 $_{(1, 77)}$	0.57	0.40 $_{(1, 82)}$	0.53	-	-

Fig. 1 Partial residual percentage parasitism of *R. fagi* on a linear predictor scale by (a) *C. nephereus*, (b) *P. longulus* in response to *F. sylvatica* trunk diameter, and (c) *C. braconius* in response to the interaction between *F. sylvatica* trunk diameter and tree position (woodland interior and edge). Fitted line from GLMM with parasitism modelled as the proportion of parasitoids per sub-sample of twenty leaves using a binomial error distribution and Logit link function.

Fig. 2 Partial residual percentage parasitism of *R. fagi* on a linear predictor scale by (a) *P. longulus* and (b) *C. nephereus* in response to habitat patch canopy area (m^2). Fitted line from GLMM with parasitism modelled as the proportion of parasitoids per sub-sample of twenty leaves using a binomial error distribution and Logit link function.

Fig. 3 Partial residual percentage parasitism of *R. fagi* on a linear predictor scale by (a) *C. braconius* in response to host density (Ln *R. fagi* +1) and (b) *P. longulus* in response to the interaction between host density (Ln *R. fagi* +1) and *F. sylvatica* tree position (woodland interior and edge). Fitted line from GLMM with parasitism modelled as the proportion of parasitoids per sub-sample of twenty leaves using a binomial error distribution and Logit link function.

Fig. 1

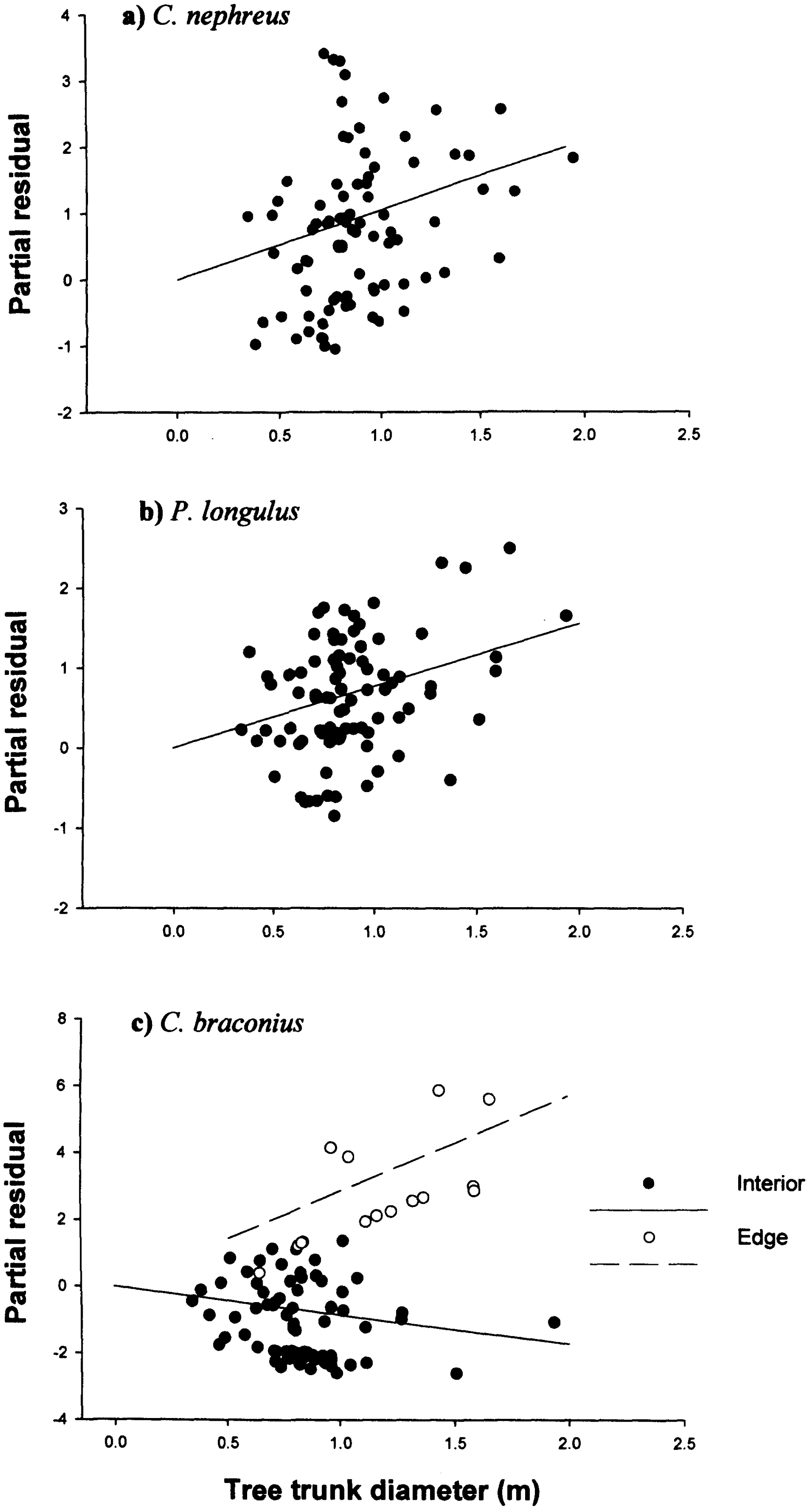

a) C. nephreus
Partial residual
4
3
2
1
0
-1
-2
0.0
0.5
1.0
1.5
2.0
2.5
b) P. longulus
Partial residual
3
2
1
0
-1
-2
0.0
0.5
1.0
1.5
2.0
2.5
c) C. braconius
Partial residual
8
6
4
2
0
-2
-4
0.0
0.5
1.0
1.5
2.0
2.5
Interior
Edge
Tree trunk diameter (m)

Fig. 2

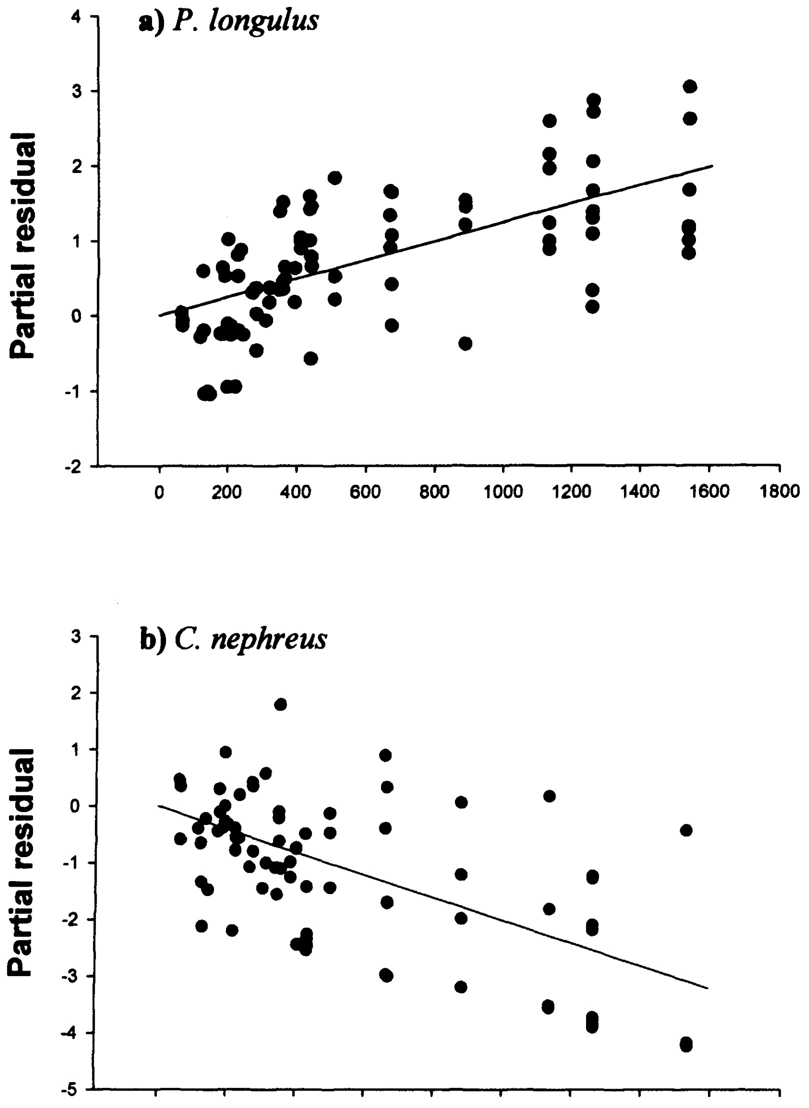
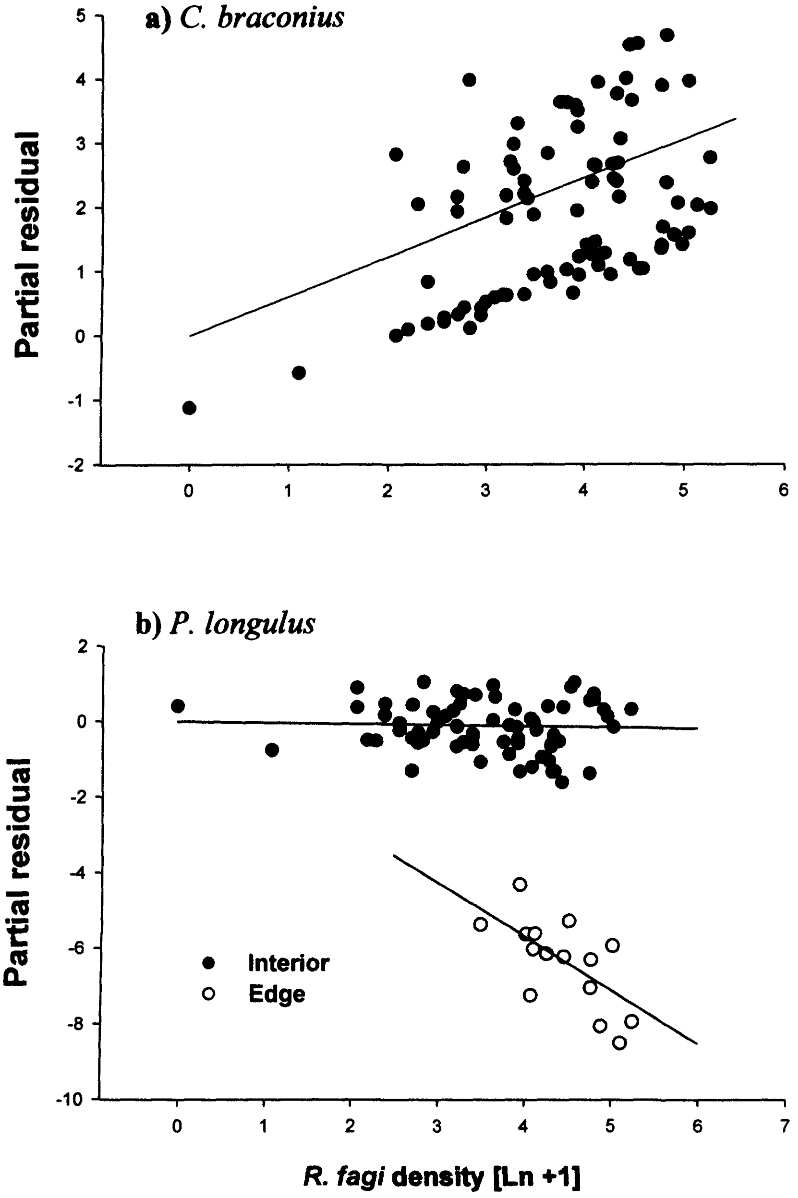

a) *P. longulus*
b) *C. nephreus*
Partial residual
Partial residual
4
3
2
1
0
-1
-2
-5
-4
-3
0
200
400
600
800
1000
1200
1400
1600
1800
Patch canopy area (m^2)

Fig. 3


a) C. braconius
Partial residual
5
4
3
2
1
0
-1
-2
0
1
2
3
4
5
6
b) P. longulus
Partial residual
2
0
-2
-4
-6
-8
-10
● Interior
○ Edge
0
1
2
3
4
5
6
7
R. fagi density [Ln +1]