THE ECOLOGY OF RIPARIAN CARABIDAE (COLEOPTERA) IN A REGULATED RIVER SYSTEM

Thesis submitted to Cardiff University for the degree of Doctor of Philosophy

by

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DECLARATION

This work has not been submitted in substance for any other degree or award at this or any other university or place of learning, nor is being submitted concurrently in candidature for any degree or other award.

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Contents

List of Figures

List of Tables

List of Appendices

Acknowledgements

Goodness me! This turned out to be harder than I had anticipated! I remember how happy I was tucking into the initial literature review; "this is a breeze," I thought. And the field work, though it was long-winded, and occasionally very wet when I waded out of my depth, was also a privilege in such a beautiful setting on the River Usk. Birds, beetles (including those I swallowed occasionally when sampling), flies, otters, sheep and cattle were good company during the long, repetitive, back-breaking hours stooped low over the cobbles with rake in one hand, aspirator in the other. Sorting and identifying thousands of beetles? Well, that *was* boring. And there are too many discarded early draft chapters to mention. I remember the day early on when I enthusiastically informed Dr. Norman Lowe that I had started a PhD: "What on *earth* do you want to do that for?" were his exact words. An early reality check! Now, saying thank you:

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Summary

Rivers and riparian zones are among the most threatened ecosystems globally, with modification of their natural flow regime a major source of change. Exposed riverine sediments (ERS) are characteristic of unregulated rivers in their upper and middle reaches and among the few remaining natural riparian habitats. However, they are in decline across the UK and Europe as a result of widespread modifications to channel structure and flow regimes. Studies of ERS and their dependent carabid beetles can help to understand how environmental change is affecting river ecosystems more generally, but prolonged research is scarce.

This thesis reports on a three year study of carabid beetles at multiple sites in the Usk river system, Wales, during an extended period of low river discharge.

Plot-scale experimentation and reach-scale surveys showed consistently that carabid assemblage structure and distribution varied more strongly in response to time and across the reach than to within-patch habitat character. There was no evidence of carabid assemblage succession, though generalist species richness appeared to increase through the study as specialist species richness declined, and general conditions for specialist species may have declined.

It is suggested that specialist carabids of high conservation importance could be squeezed as land use encroachment and river regulation causes a decline in the ERS resource. Management interventions at the reach- or catchment scale are advocated to maintain and restore the ephemerality of ERS. Being responsive to reach- and catchment scale events, exposed riverine sediments and their dependent fauna should be the focus of long term study to appraise rates of environmental change or resilience to anthropogenic stressors. In particular, long term studies may not only reveal trends on ERS towards homogenisation, indicative of environmental decline within the wider river system, but might also help to detect the effectiveness of river restoration.

1 General Introduction

1.1 The River Environment

Although disproportionately rich in biodiversity, rivers are among the most threatened ecosystems globally (Paetzold *et al.* 2008). In their natural, unmodified state, rivers are typically highly dynamic hydrologically, perpetually exposed to and recovering from events created by rainstorms or snow melt (Rabeni and Sowa 2002). Riverine organisms respond to these hydrological variations over timescales ranging from individual events, for example by short term avoidance movement, through seasonal migration, to the evolutionary scale, by adapting their life cycles or occupying niches created by the resulting habitat template (Townsend and Hildrew 1994; Thorp *et al.* 2006). Habitat conditions vary longitudinally along the river continuum (Tomanova *et al.* 2007) and also laterally across the ecotone where river channel gives way to floodplain or riparian zones (Arscott *et al.* 2005; Tomanova *et al.* 2007).

While natural flow regimes maintain dynamic river and riparian ecosystems (Van Looy *et al.* 2007), rivers are also subject to a range of physical modifications, for example impoundment, abstraction and canalisation with consequences for habitat availability and altered flow pattern (Rabeni and Sowa 2002). Also, physico-chemical alterations arise from nutrient runoff, acidification, and sedimentation from altered land use and management (Pye *et al.* 2012; Larsen and Ormerod 2014). In Europe, modifications arise wherever river catchments are exploited for productive use, with mountain-to-lowland rivers among the most altered from their natural state (Jahnig *et al.* 2009a). The importance of these effects on rivers is apparent from the large number of river and floodplain restoration projects currently underway in response to the Water Framework Directive requirements for holistic, integrated management (EC 2000). In the UK and Wales specifically, the UK National Ecosystem Assessment reported that, judged against a 1995 baseline, rural rivers exhibited a decline in water quality from very good to good, while climate change is expected to affect Wales's freshwater ecosystems further (NEA 2011). Upland rivers, however, showed a recovery from acidification (Ormerod and

Durance 2009) and the chemical quality of Britain's rivers has improved since the 1980s. Biological and chemical classifications of the formerly most polluted rivers had improved since the 1990s, especially in urban areas; with some uncertainty over recent declines in water quality in some of Wales's highest quality rivers (NEA 2011).

1.2 Exposed Riverine Sediments

Within the dynamic river environment of the UK, exposed riverine sediments (ERS) are one of the few remaining, relatively natural riparian habitats (Bates and Sadler 2005; Bates *et al.* 2005), and form in response to fluvial and sediment dynamics. They comprise areas of exposed cobbles, shingle and sand defined as "*exposed within channel fluvially deposited sediments (gravels, sands and silts) that lack continuous vegetation cover, whose vertical distribution lies between the levels of bankfull and the river's typical baseflow*," (Bates and Sadler 2005) (*Figure 1.1*). Owing to their position at the margin of the wetted channel and surrounding terrestrial landscape, ERS provide an interesting opportunity in which to understand how combinations of natural and anthropogenic landscape processes occur over a range of spatial scales and time-frames to affect the species richness, composition and distribution of specialist organisms (Framenau *et al.* 2002; Bates *et al.* 2005; Parsons and Thoms 2007; Reese and Batzer 2007; Tomanova *et al.* 2007; Tomanova *et al.* 2007). The large array of micro-habitats available within ERS along gradients of disturbance, succession, temperature, humidity, inundation frequency and availability of aquatic food subsidies, presents opportunities for understanding aspects of ecological processes. These include colonisation, succession and competition within this dynamic riverine environment (Bates *et al.* 2007b). Studies can be targeted at particular zones, such as the foreshore, and by manipulation of different variables.

1.3 Conservation of ERS and their Specialist Fauna

As with many other groups of riverine organisms, there is increasing interest in the conservation of ERS in accordance with UK biodiversity conservation objectives (UKBAP 1999; Eyre *et al.* 2001; Eyre and Luff 2002b; Eyre and Luff 2002a; Eyre *et al.* 2002; Sadler and Bell 2002; Sadler *et al.* 2004; Bates and Sadler 2005; Eyre 2006; Bates *et al.* 2007a;

Larsen *et al.* 2009). In 1999, the UK Biodiversity Group prepared a Species Action Plan grouping six species of ERS Coleoptera specialised for this habitat. These were three Carabidae, two Staphylinidae and one Hydrophilidae, which share specific and exclusive traits for ERS, including their mainly western Britain distribution and reliance on shingle-type exposures (UKBG 1999). The preparation of this original plan was followed by joint survey and conservation management projects co-ordinated between the nature conservation agencies and regulatory sector, made up at that time of Scottish Natural Heritage, The Countryside Council for Wales, English Nature and The Environment Agency (Sadler and Bell 2000; Eyre *et al.* 2001; Eyre and Luff 2002b; Bates and Sadler 2005). These projects indicated that habitat turnover, spatial and temporal variation in patch quality, and resource distribution exerted selection pressures on the animals of ERS (Bates *et al.* 2006). Whilst such findings might apply to any group of animals, they highlighted the relationship between specialist organisms and these hitherto overlooked ephemeral habitats.

Owing to their widespread distribution, specialised and generalist traits, and rapid response to environmental change, terrestrial Carabidae (Coleoptera) provide potentially important bio-indicators of the effects of environmental change on ecosystem function and the persistence of suitable environmental conditions for specialist fauna (Eyre 2006; Horn and Ulyshen 2009). Moreover, where species are specialists of ERS with restricted distributions, beetles provide ideal study subjects to help elucidate the ecological changes underway on site. For example, Carabidae are sensitive to changes in grain size, sediment moisture levels and food availability (Andersen 1978; Manderbach and Hering 2001; Bates *et al.* 2007b), each of which will be affected on ERS by river discharge levels and inundation events. Whilst research has focussed on the conservation of specialist species, their relationship with ERS might also help to understand wider changes in the riverine landscape.

Figure 1.1 Two examples of exposed riverine sediments on the River Usk, an ‘island bar’ mid-stream (a) and a ‘lateral bar’ on one bank of the river (b). See also *Figure 2.1*.

Despite this recent interest in ERS, there remains limited understanding of the ecological consequences of natural and anthropogenic river dynamics on ERS Carabidae. Whilst evidence is emerging of adverse consequences for wildlife within modified floodplains (Larsen *et al.* 2009; Larsen *et al.* 2011; Larsen 2010; Larsen and Ormerod 2014), insufficient background data mean that contemporary efforts to conserve and restore riparian ecosystems are undertaken with little understanding of the key processes affecting ERS and their organisms (Jahnig *et al.* 2009a; Jahnig *et al.* 2009b; Acreman and Ferguson 2010). Therefore, to increase understanding of ERS and their specialist organisms, this study set out to test the general hypothesis that environmental change (habitat succession, river discharge) affects the distribution of specialist Carabidae assemblages on ERS at a range of spatial and temporal scales.

To investigate this hypothesis, the thesis is structured as follows:

> Chapter 2 provides a literature review, outlining the vulnerability of riparian zones to ecological decline in response to anthropogenic and climate change, and reviews the ecology and habitat dynamics of exposed riverine sediments and their specialist Carabidae (ERS specialists) within the riparian zone.
>
> Chapter 3 provides a preliminary evaluation of two principal sampling techniques used on ERS, pitfall traps and timed hand searches, to identify the preferred method for a three year, multi-sample and multi-site survey described in subsequent chapters.
>
> Chapter 4 examines the distribution and abundance of carabid beetles on ERS opportunistically in the catchment of the River Usk, Wales (UK), over a three year period, during which annual river discharge declined year-on-year and no inundation events occurred. The study tests the hypothesis that local habitat character had larger effects on carabid assemblages than variations within and between years.
>
> Chapter 5 tests the hypothesis that successive periods of low river discharge will be accompanied by ecological succession within ERS carabid assemblages in the knowledge that the dynamics of ERS should interrupt faunal succession where it

occurs, so evidence that it persisted would indicate increasing stability, and reduced suitability for ERS specialists.

Chapter 6 uses a habitat manipulation experiment to investigate the hypothesis that enhanced food availability, leaf litter and distance from water influence the micro-spatial distribution of ERS specialists. The intention was to examine whether these local, short term interventions, targeting ERS beetle behaviour, produced stronger effects than larger-scale environmental variations.

Chapter 7 considers the results in a wider management context and makes recommendations for further research.

1.4 Description of the Study Site

1.4.1 Study Area: A Regulated Riverine Environment

The study was conducted in the temperate and relatively maritime region of NW Europe, specifically within the River Usk in the Brecon Beacons National Park, Wales (Ordnance Survey grid references SO31002252 to SO31162243, *Figure 1.2*). In this formerly glaciated landscape, the Usk is an important near-natural feature forming a continuous linear habitat from west to east within an otherwise agricultural landscape where other near-natural habitats are highly fragmented. It is fed by numerous tributaries that rise and incise through the uplands to the north and south of the floodplain. It is classified as over-licensed for water abstraction (EAW 2007). This means that if all abstraction licences issued were used to their full allocation, this would cause unacceptable environmental damage to the river at low flows. To emphasise this point, further downstream from the study area there is already a risk that unacceptable damage is being caused to the river as a consequence of abstraction levels.

The river water quality in terms of chemistry, biology and pollutants upstream, and within the vicinity of the study area, is classified as generally very good (EAW 2008). The ecological status of the river is classified as good rather than very good because river morphology has been modified by human intervention (e.g., dredging and river bank

Figure 1.2 The study area □ situated on the River Usk Special Area of Conservation, within the Brecon Beacons National Park, Wales.

alterations) (EAW 2009). The river discharge responds closely to rainfall patterns (*Figure 1.3*) and is regulated by impoundment and abstraction (DCWW 2014). For the purposes of this study, these factors mean that the River Usk is considered to be modified, with the assumption that other river and environmental processes affecting the ecological dynamics of ERS are modified too.

The River Usk rises to the west on the Mynydd Du Common within the Fforest Fawr Geopark (Ordnance Survey grid reference SN81852389), at 500m above ordnance datum (AOD), flowing into the Usk Reservoir, one of a number of headwater impoundments within the Usk catchment. It then flows eastwards and south-east from which point it is designated as a Special Area of Conservation (SAC) and Site of Special Scientific Interest (SSSI), through a predominantly agricultural landscape mainly of pasture. It flows across predominantly Devonian Old Red Sandstone bedrock. Upstream of the study area the riverbanks are mostly tree-lined with ash (*Fraxinus excelsior*), alder (*Alnus glutinosa*), oak (*Quercus petraea*) and willows (*Salix* species) shading often steep and rocky sections. Upstream of the study area numerous ERS are visible from aerial photographs. The river passes through characteristic upper, middle and lower reaches (Power and Rainey 2000), with nutrient-poor headwaters in the more rocky and peaty upland zone becoming increasingly nutrient-rich downstream.

The SAC is designated for several species of freshwater fish, otter (*Lutra lutra*) and freshwater crowfoot (Ranunculaceae). Owing to the presence of physical barriers to fish migration such as weirs, as well as depletion of river flow, localised pollution incidents and an abundance of invasive non-native riparian plant species, most of the features for which the SAC is designated are reported to be in an unfavourable conservation status (CCW 2009). The SSSI is designated for the same features as well as for separate features of importance in an UK context, including a variety of rare and scarce mosses, liverworts and invertebrates (flies, spiders and beetles) associated with ERS. Within the Severn River Basin District (EA 2009), river restoration is recognised as a priority for the Upper Usk and Wye catchments in Wales (EAW 2010).

The study area (*Figure 1.2*) falls within the middle reaches of the River Usk, which includes exposed and steep river banks, meandering pools, riffles, cobbles and gravels, where naturally occurring events include riverbed-scouring floods and shifted sediments (CCW 2009). As a consequence of the narrow floodplain flanked by high hills and mountains covered by thin soils or degraded blanket bog and wet heath, as well as a significant absence of woodland (Larsen *et al.* 2009), the river floods during prolonged and heavy rainfall, inundating the surrounding floodplain and study area (*Figure 1.4*).

National Parks in Britain are listed as Category V Protected Landscapes by the International Union for the Conservation of Nature (IUCN). This category describes protected areas where the interaction of people and nature over time has produced an area of distinct character with significant ecological, biological, cultural and scenic value; and where safeguarding the integrity of this interaction is vital to protecting and sustaining the area, and its associated nature conservation and other values. The primary objective for these areas is to protect and sustain important landscapes/seascapes, along with the associated nature conservation and other values created by interactions with humans through traditional management practices. River ecosystems within a National Park might be assumed to possess high biodiversity and ecological processes representative of the high conservation value of the protected landscape. Based on the knowledge that river floodplains are relatively rich in biodiversity, main rivers such as the River Usk are likely to be comparatively ecologically diverse and important in terms of ecosystem goods and services provided. For example, the catchment used in this study is a principal source of drinking water for approximately 750,000 people in south and east Wales (DCWW 2014), just under 25% of the country's population. Yet the frequent impoundments will affect its ecology and lead potentially to the loss of biodiversity (Rolls *et al.* 2012). High levels of river regulation, and recent downward revisions to the permissible volumes of annual abstraction (DCWW 2014), underline a need to develop a better understanding of what defines high quality river habitat and Favourable Conservation Status (EC 1992). This study contributes to that understanding and to the role that ERS can play as status sentinels.

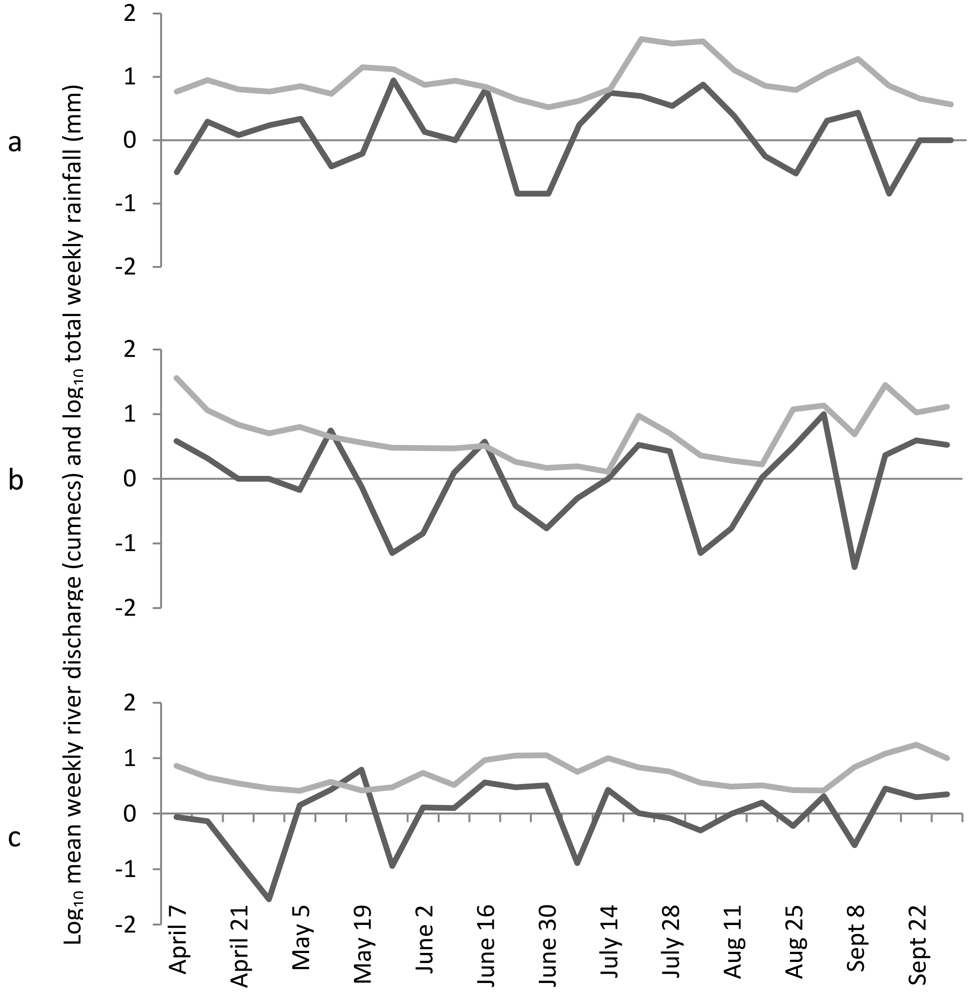


Figure 1.3 Variations in river discharge and rainfall on the River Usk during the study season April to September in a) 2009, b) 2010 and c) 2011. ▬ Log_{10} mean weekly river discharge (cumecs) recorded at Llandetty (Ordnance Survey grid ref SO31262203) approximately 5 km downstream of the study area; and ▬ Log_{10} total weekly rainfall (mm) recorded at the Natural Resources Wales weather station at Velindre, approximately 12 km north-east of the study area (SO31842367).

Figure 1.4 Flooding during September 5th 2008, inundating the most upstream study site, Site 1 (see Chapters 3, 4) beyond the line of trees in the mid-background, viewed from the south west. This was the only time during 2008 to 2011 that the survey area experienced this level of wholly immersive flooding. Photo by kind permission of Chris Alford, landowner.

2 Environmental Change and the Carabidae (Coleoptera) of Exposed Riverine Sediments: A Literature Review

Summary

Natural river ecosystems have high biodiversity as a consequence of their spatial and temporal complexity. They are, however, undergoing rapid change globally through modifications to their catchments, riparian zones and channels. The riparian zone is particularly important for exchanges of energy, nutrients, water and organisms, with the surrounding landscape and research in this zone providing insight into processes connecting rivers with the floodplain. This review focuses on exposed riverine sediments (ERS) as one specific and well-defined riparian habitat. It describes i) their assemblages of specialist ground beetles; ii) their response to changing hydro-geomorphology and river discharge; and iii) their value as indicators of wider ecological changes within temperate river ecosystems.

In terms of geomorphology, ERS are point, lateral and island bars composed of graded sediments ranging from sands and gravels to cobbles and boulders. Their distribution is regulated by river discharge, sediment exchange and transport. They are vulnerable to anthropogenic influences on these factors. In the UK, they are distributed mainly on unregulated rivers in Wales, south-west and north-west England and Scotland but their extent is now declining as a consequence of anthropogenic change and regulation within catchments.

Most research on ERS during the past decade has focused on population processes, distribution and life-history traits of the specialist Carabidae in order to understand their conservation value. These are summarised in this review. Less attention has been given to assessing and understanding how regulation and flow dynamics affect ERS and their specialist organisms. Research needs to be directed towards understanding what ERS and their specialist fauna indicate about habitat connectivity within the floodplain; to chart the changing conservation value of river channels on ERS; the scale of factors influencing assemblage distribution; and hence the scale at which restorative intervention is best achieved. Exploring this is an important research priority to improve the ecological restoration of the UK's river ecosystems.

Key words: Anthropogenic, Brecon Beacons National Park, Regulation, Riparian Squeeze, River Usk, Scale, Stressors.

2.1 Introduction

Wetlands and their biodiversity, including upland and lowland bogs, fens, ponds, inland and coastal swamps, marshes and other intertidal areas, and rivers and floodplains, provide a range of ecosystem services. These include flood alleviation, absorbing pollution and sediment, recycling nutrients, sequestering carbon, recharging groundwater, providing peat and minerals, and providing water for irrigation and consumption (Hartig *et al.* 1997; Zedler and Kercher 2005); all are reduced in efficiency and contribution when wetlands are damaged or lost (Zedler and Kercher 2005). Although rivers, lakes and wetlands support a disproportionately high number of the Earth's species (Arscott *et al.* 2005; Dudgeon *et al.* 2006), they are among the most threatened ecosystems, mainly as a consequence of human exploitation, modification and regulation (Paetzold *et al.* 2008; Tockner *et al.* 2010). Globally during the past two centuries, wetlands have declined to about half their original area (Zedler and Kercher 2005), whilst in Europe they have declined to just 20% of their original area during the past millennium (Verhoeven 2014). For example, 90% of floodplains in Europe and North America are cultivated and therefore functionally extinct as wetlands (Tockner and Stanford 2002). River ecosystems and floodplains are characterised by high spatial and temporal heterogeneity which underpin their ecological complexity, and affect the diversity and distribution of living organisms (Ward *et al.* 1999; Paetzold *et al.* 2008; Tockner *et al.* 2010). Little, however, is known about how downstream changes in the physical structure and hydrological dynamics of rivers affect ecological function (Arscott *et al.* 2005). Additionally, rivers and floodplains are particularly susceptible to the effects of climate change because their hydrological and thermal regimes reflect regional climatic conditions (Erwin 2009). Climatic effects on rivers also interact with other stressors such as river regulation, abstraction and canalisation (Strayer and Findlay 2010; Rolls *et al.* 2012; Thomas 2014). River sensitivity to environmental change and habitat fragmentation emphasises the need to identify the appropriate scale at which to investigate river and floodplain ecology in order to advise management (Clews 2007; Tockner *et al.* 2010). In particular, there is a need to identify specific habitat patches and ecotones that provide a synoptic indication either of deterioration or progress towards management objectives across the wider catchment.

This review focuses on environmental change in the riparian zone, in particular on the highly dynamic exposed riverine sediments (ERS) and their specialist invertebrate fauna. As a declining habitat type whose distribution and evolution respond directly to river discharge and anthropogenic change, ERS provide readily definable patches to direct research that might provide the synoptic indications of change outlined above. The review summarises what is understood about ERS and how specialist Carabidae (Coleoptera), which dominate invertebrate fauna by rarity and abundance (Bates and Sadler 2005; O'Callaghan *et al.* 2013b), are distributed on them in response to environmental variation. Moving beyond the recent focus on the conservation of ERS and their specialist fauna *per se* (Bates and Sadler 2005; Bates *et al.* 2005; Sadler *et al.* 2006; Bates *et al.* 2009), the review also identifies the potential to broaden the role of ERS-based research and Carabidae dynamics to understand how the riparian zone responds during rapid environmental change.

2.2 Riparian Zones within River Ecosystems

The complexity and diversity of river systems are exemplified in the riparian zone (Strayer and Findlay 2010). Recent emphasis on the ecological effects of human intervention and low flow on river ecosystems (Van Looy *et al.* 2007; Rolls *et al.* 2012), lends weight to focussing on changes in the riparian zone in order to understand wider changes within the floodplain. It also supports focusing on consequential effects on the extent and condition of aquatic and terrestrial habitat, species distribution patterns, energy and materials exchanges, and habitat fragmentation. In this ecotone, physical energy is dissipated, and energy, nutrients, water and materials are exchanged, moderated by geology, hydrology, biology and climate. Anthropogenic stressors have limited and reduced these dynamics, leading to ‘riparian squeeze,’ where water flow and quality, as well as the extent, range and ecological function of riparian habitats, are reduced, laterally compressing and stabilising the zone (Strayer and Findlay 2010). Recent research has focussed on identifying the spatio-temporal scales at which change occurs and consequently the scale, local, reach or catchment, at which management is most effectively applied. For example, sediment deposition, reflecting local or reach scale habitat change, altered river invertebrate composition (Larsen *et al.* 2009) so that those fauna with susceptible life-history traits responded adversely to habitat modification at different scales (Larsen and Ormerod 2010). In contrast, reach- and catchment-scale riparian habitat restoration led to scale-dependent responses by organisms in aquatic habitats (Clews *et al.* 2010); and aquatic invertebrate assemblages differed in response to the habitat type bisected by the streams examined (Thomas 2014). To date, research on scale-dependent responses by organisms in other riparian habitats, such as ERS, is lacking.

2.3 Exposed Riverine Sediments within the Riparian Zone

Within the riparian zone, exposed riverine sediments (ERS) are exceptionally dynamic habitats where physical and biological changes occur rapidly within a confined area (Bates *et al.* 2009). Defined as "*exposed within channel fluvially deposited sediments (gravels, sands and silts) that lack continuous vegetation cover, whose vertical distribution lies between the levels of bankfull and the river's typical baseflow*" (Bates and Sadler 2005), ERS respond directly to changes in river discharge and hydro-geomorphology. Consequently, they are vulnerable to the effects of riparian squeeze. They are "*highly disturbed, naturally patchy and regularly distributed*" with "*strongly adapted specialists*" living on them (Bates *et al.* 2006). Exposed riverine sediments abundance within a catchment is related to seasonal flow regimes, substrate type and montane headwaters that provide high energy conditions and levels of disturbance to maintain and rejuvenate them. Their area is inversely related to the prevalence of headwater abstraction (O'Callaghan *et al.* 2013b). In Britain, ERS occur mainly in Wales, south-west and northern England and Scotland, on unregulated rivers (Eyre *et al.* 2001; Eyre and Luff 2002b; Eyre and Luff 2002a; Eyre *et al.* 2002; Sadler and Bell 2002; Sadler *et al.* 2004; Bates and Sadler 2005), where higher altitude headwaters flow across mainly glacial or water-distributed sediments (O'Callaghan *et al.* 2013b). These latter authors further noted that, as a consequence of river engineering, ERS have disappeared from most of the UK and mainland Europe’s rivers (canalisation, dredging, water abstraction, impoundment etc.). Thus, the extent and number of ERS within a river indicate the extent to which a river maintains a level of ‘naturalness’ and therefore provide potentially vital, as well as physically visible, sentinels on the ecological status of a floodplain.

Occurring as point bars inside a meander bend, lateral bars on a straight river section and island bars surrounded by water (Sadler *et al.* 2006) (*Figure 2.1*), ERS should be in a state of dynamic equilibrium with river levels that remain high enough to provide regular, powerful water flows to re-work the sediments and prevent vegetative succession (Bates and Sadler 2005). Generally, ERS are rejuvenated and redistributed by floods, and stabilised and reduced in area by vegetation succession. On the basis that some exposed sediments only remain devoid of ground cover as a consequence of livestock trampling, the ERS definition above includes eroding river banks but excludes riffle tops, exposed river bed and bank-top deposits, as well as open sediments within oxbows and cut offs (Bates and Sadler 2005). It therefore does not account for the potential effects of prolonged low flows occurring as a consequence of the combined influences of meteorological change and river regulation. These circumstances might lead to quasi-permanent exposure of river beds, shoals and riffle tops that might prove suitable to specialist ERS fauna. The definition also does not account for faunal behavioural and dispersal responses to these changes, and potential faunal and structural interchange between locations, moderated by fluctuating river discharge.

2.4 ERS Specialist Fauna

True flies (Diptera), spiders (Araneae), ants (Formicidae) bugs (Hemiptera) and beetles (Carabidae) are the main invertebrate classes of ERS, with Carabidae dominating by number of habitat specialists and rarity, and probably by abundance and biomass too (Bates and Sadler 2005; O'Callaghan *et al.* 2013b). Rarity recorded in Britain (Bates *et al.* 2009) mirrors that recorded in mainland Europe and Scandinavia (Manderbach and Reich 1995; Andersen and Hanssen 2005). Whilst there is some published information about habitat preferences and responses to food availability and flooding by Araneae (Power and Rainey 2000; Framenau *et al.* 2002; Paetzold and Tockner 2005; Henshall *et al.* 2011), most published information on organism life history traits for ERS relates to Carabidae, though this remains poorly understood. Exposed riverine sediments are, however, also of importance for bird breeding cycles (Yalden 1986; Lloyd and Friese 2013).

2.4.1 Traits of Carabidae on ERS

Many studies comment on the suitability of Carabidae (Coleoptera) for studying ecological change by virtue of their life history traits, and their abundance and distribution through most habitats (e.g., Boscaini *et al.* 2000; Cardenas and Hidalgo 2007; Horn and Ulyshen 2009). Additionally on ERS, the number of specialist species present also emphasises site suitability (Bates *et al.* 2005). Provided that there is regular flooding, riparian Carabidae appear throughout the river system (Lambeets *et al.* 2008a; 2008b; 2009) with sediment-specialist xerophiles such as *Paranchus albipes* and *Agonum micans*, supplemented by hygrophiles requiring damper sediments and/or vegetation cover, such as *Lionychus quadrillum, Amara aulica,* and *Calathus fuscipes*.

Studies of Carabidae on ERS and in the riparian zone have described species according to their biology and the environmental conditions in which they occur (Van Looy *et al.* 2007), relating species phenology and distribution to vegetation cover and substrate type (Andersen 1985a; Bates *et al.* 2007b), describing their tendency to disperse by walking or flight (Bonn and Helling 1997; Bates *et al.* 2006), and their tolerance to changing soil moisture levels (Bates *et al.* 2007b; Lambeets *et al.* 2008a). Most species of Carabidae occur within a limited range of soil moisture conditions, with this and micro-climate humidity being the most important factors in their distribution (Luff 2007). Numerous Carabidae are ERS specialists by virtue of their adaptive traits (*Table 7.1, Appendix 4*) (Andersen 1985a; Bonn and Helling 1997; Framenau *et al.* 2002; Bates and Sadler 2005; Sadler *et al.* 2006; Bates *et al.* 2007b; Lambeets *et al.* 2008a; Horn and Ulyshen 2009; Jahnig *et al.* 2009a) and the fact that some species are recorded more frequently on ERS than on other habitats (Fowles 2004). Between 10 to 40 species are usually active within a habitat during any one season (Lovei and Sunderland 1996). Micro-spatial distribution within a habitat patch is likely to be influenced by habitat heterogeneity and inter-specific competition (Bates *et al.* 2007b).

Studies on the River Severn in Wales have found a limited number of *Bembidion* species dominating assemblages in high numbers and occupying many study sites (Sadler *et al.* 2006). Life cycles of various *Bembidion* species remain constant irrespective of climatic variations between years or locations, with other species showing biennial or plastic lifecycles (Andersen 1983a, b). Most *Bembidion* species hibernate as adults over winter and life cycles are completed earlier in the year in cooler climates (Andersen 1983b).

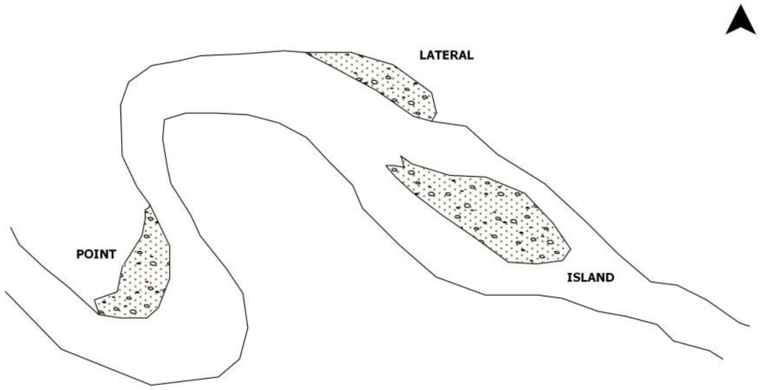


Figure 2.1 Illustration of idealised point, lateral and island 'bars' of exposed riverine sediments (ERS) along a river, each of which were included in this study.

Bembidion species live mainly near water and are either nocturnal or diurnal (Luff 2007). Numerous studies have elucidated the habitat preferences of different *Bembidion* species and other Carabidae. Some species show preferences for larger or smaller grain size irrespective of moisture content (Andersen 1978; Manderbach and Hering 2001; Bates and Sadler 2005; Bates *et al.* 2006; Sadler *et al.* 2006; Bates *et al.* 2007a; Kleinwaechter and Rickfelder 2007; Kleinwachter and Burkel 2008). Exposed riverine sediments range in size from cobbles through shingles to sands. Some species prefer interstitial spaces (Andersen 1985a, b, 2006) or spaces beneath vegetation (Martin *et al.* 2001). Both positive and negative phototaxes have been demonstrated under different temperature regimes (Andersen 1989, 2006), as well as different responses to temperature and heat stress (Andersen 1986), and to moisture and humidity (Andersen 1968, 1970, 1985a; Evans 1997). Responses to vibration (thigmokinesis) (Andersen 1985b) and preferences for chemical responses associated with preferred sediments sizes and locations (Evans 1988) have also all been demonstrated. As r-strategists with high dispersal ability, ERS specialists, the majority of which are winged, can find and colonise small ERS patches (Jahnig *et al.* 2009b). This indicates that ERS specialists, which might be sensitive to changes in the hydro-geomorphological regimes governing ERS availability, can disperse readily to other suitable patches.

This range of responses by different species can be attributed to different seasonal and habitat traits; this also expresses regional variation. For example, responses might include movement towards heat and light during the warmer summer, and away from heat and light, and towards drier conditions, during the autumn hibernation season. Alternatively, they might include movement towards or away from shadows cast by vegetation (preferences for cover or open ground); and towards chemical stimuli for short-range feeding, mating and resting, or long-range stimuli for habitat selection. These preferences are presumed to prolong the survival and fitness of species exploiting transient, patchy, heterogeneous and dynamic environments.

2.5 Anthropogenic Stressors of the Riparian Zone and ERS

Anthropogenic stressors of the riparian zone and ERS include disturbance to organisms and soil erosion from livestock trampling; aggregate abstraction; channelisation (e.g., river flood defences); water abstraction; flow regulation (impoundment); sediment loading; pollution (e.g., agricultural runoff); recreational activities and climate change (e.g., changes to precipitation rates, intensity and seasonality) (Bates *et al.* 2007a; 2007b; Paetzold *et al.* 2008; Larsen *et al.* 2009; Strayer and Findlay 2010). O'Callaghan *et al.* (2013) explain that headwater impoundment and abstraction are principal drivers of ERS distribution change. Both can alter the interactions between river discharge and sediment transport power, reducing the range and frequency of high river discharge that drives the re-sorting and scouring of sediments. Impoundment also traps sediments, thereby altering the balance of erosion and deposition (Gurnell *et al.* 2009). Sediment abstraction and land use changes alter the rate of sediment supply to rivers (Kondolf *et al.* 2002; Liebault and Piegay 2002).

Another potential stressor is the supplanting of native plant species by invasive non-native species (INNS) such as Japanese knotweed, *Fallopia japonica*, and Himalayan balsam *Impatiens glandulifera*. Though there is not yet sufficient published evidence, it is likely that encroachment of Himalayan balsam along riverbanks is interfering with river hydro-geomorphology and potentially ERS formation. Interference would include increasing soil erosion (Greenwood *et al.* 2013) and altering the rate of sediment accumulation and vegetation establishment, which are integral to natural channel regulation processes (Gergely *et al.* 2001; Bertoldi *et al.* 2011; Gurnell *et al.* 2012).

Whereas the above factors interfere with the availability and distribution of ERS, species richness amongst ERS specialist Carabidae is associated with ERS size (area) and availability of aquatic food subsidies (Jahnig *et al.* 2009b). The latter and the rate of transfer of essential resources to specialist organisms across the aquatic terrestrial ecotone are positively associated with flood events (Schneider *et al.* 2002; Paetzold *et al.* 2005; Ballinger and Lake 2006). Paetzold *et al.* (2008) explain that anthropogenic stressors, such as the release of fine sediments, exert a negative impact on the abundance and species richness of arthropod assemblages by reducing the availability of interstitial spaces between coarser sediments.

Given their reliance on regular scouring and re-sorting from "structural flows" (O'Callaghan *et al.* 2013b) to maintain exposed sediments, a particularly important stressor of ERS is low river discharge. Whereas regular flood events facilitate nutrient transfer, which invigorates terrestrial predator species richness, the reverse may be true of low river discharge (Rolls *et al.* 2012). Critical competition thresholds between ERS specialists are normally avoided because the dynamic, spatial and temporal redistribution of micro-habitats by flooding, succession and lower order inundation events maintain habitat and assemblage heterogeneity (Bates and Sadler 2005). It is possible, therefore, that inter-specific competition, which might be inhibited by regular disturbance events because population densities crash and recover (Wilson and Thomas 2002), might increase as population densities grow during prolonged periods of stability. Low flows also mediate the exposure of new sediments, which may supply new food subsidies stranded by retreating flow. It is, however, also possible that higher population densities might lead to dominance by fewer species most able to respond to spatio-temporal homeostasis.

2.6 Conclusions and Evidence Gaps

The ecological importance and high biodiversity of riparian ecotones is exemplified by their range of associated specialist and opportunistic organisms, their high physical, spatial and temporal complexity and connectivity mediated by river discharge (Ballinger and Lake 2006; Strayer and Findlay 2010; O'Callaghan *et al.* 2013b), and the exchange of energy, water, nutrients and organisms. The vulnerability of riverine ecosystems and floodplains to anthropogenic change is well documented; this threatens their very high contribution towards global biodiversity, and ecosystem goods and services provided. The extent and rate of change can be studied in the riparian zone, where ERS, which themselves are in decline in Wales and England, provide highly visible locations for such study. The current definition of ERS may need to be amended to reflect environmental conditions in modern regulated rivers and faunal responses to these conditions. It may, however, still be possible to track structural and distribution traits of faunal assemblage patterns in response to ERS traits in a regulated or otherwise changing environment. Given that specialist species are in decline globally and are being supplanted by generalist species (Clavel *et al.* 2011), it might also be possible to chart the changing conservation value of river channels on ERS.

Faunal distribution is influenced by habitat distribution, proximity and succession (Compton 2002; Baguette and Van Dyck 2007). The responses of invertebrate assemblages reliant upon specialised or transient habitats such as ERS provide a measure of the rate of spatial and temporal habitat change within a floodplain (Lambeets *et al.* 2008b; Larsen *et al.* 2009). Whilst ERS are a regular feature of unregulated rivers, regulation may alter their distribution and, consequently, faunal assemblage distribution patterns and structure too. It follows that where Carabidae assemblages on ERS in unregulated rivers indicate the level of connectedness to the wider floodplain, in a regulated river it should be equally possible to understand connectedness; a first step towards this interpretation is to understand the scale at which faunal responses to environmental change occur.

Whereas ERS have so far been studied in terms of their contribution towards biodiversity conservation and declining refuges for specialist fauna, ERS-based research now needs to be directed towards understanding how the riparian zone responds during rapid environmental change (O'Callaghan *et al.* 2013b). There is a paucity of multi-year studies of ERS or Carabidae (Gereben 1994; Sadler *et al.* 2006; Van Looy *et al.* 2007) that shed light on the spatio-temporal scale at which specialist and opportunistic fauna respond to environmental change. There is also a paucity of investigations of survey methods that might be appropriate for a multi-site, multi-sample and potentially long term study. The present study was designed with all these evidence gaps in mind.

3 Comparing Two Techniques for Sampling Carabidae (Coleoptera) on Exposed Riverine Sediments

Summary

Invertebrate sampling techniques in any environment should ideally sample assemblages representatively and reliably, with sufficient precision to detect change or variation. Specific challenges sometimes arise however, in habitats or taxa characterised by marked dynamism or frequent movement. Both of these effects are possible whilst sampling the specialist invertebrates of exposed riverine sediments (ERS) because of repeated floodwater inundation.

In preparation for a more prolonged investigation, this study compared the representativeness and reliability of two popular sampling techniques for studying the distribution of assemblages of Carabidae (Coleoptera) on exposed riverine sediment sites: traditional pitfall traps (n = 9 pitfall trap grids) and constant-effort hand searches (n = 13 sample locations) were compared over a period of one month on two separate ERS patches. Hand searches were adapted by using a hand rake to achieve rapid, even exposure of requisite sediments. Pooling data by site for each technique, they were compared using t-tests, GLM and the Kruskall-Wallis test to appraise differences in species richness, abundance, richness and abundance of specialist species, and mean richness and abundance per species per technique. Sorensen's Similarity Index was used to compare site representativeness by each technique. Rarefaction curves were used to confirm that the techniques had sampled the majority of species available.

Totals of 220 individuals of 23 species of Carabidae were sampled by the two techniques. Timed hand searches produced higher species richness and abundance than pitfall traps. They also recorded a significantly higher proportion of ERS specialist species and produced the greater abundance. Timed hand searches distinguished between sites by proportion of ERS specialist species; they sampled a higher mean abundance per specialist species and achieved higher inter-site assemblage similarity than pitfall traps. For a longer three year survey of multiple sites, during which 12 specialist species were recorded, timed hand searches produced ten of these within the first eight sample locations during the first year, and during the first 80 minutes of a 90 hour sampling season. Timed hand searches were, therefore, a more robust, reliable and representative technique than pitfall traps for sampling ERS specialists within a spatially and temporally dynamic activity zone. Higher species richness and more rapid species accretion with sampling effort in pitfall traps was attributable to a higher proportion of generalist Carabidae, but the additional time cost required in pitfall traps relative to the number of ERS specialists recorded meant that this approach was not favoured for such a large survey as that required during years following this initial comparison.

Key words: Beetles, *Bembidion*, Hand Search, Insects, Pitfall Trap, Rarefaction, Riparian, River Usk.

3.1 Introduction

Understanding the vulnerability of river riparian zones to global change and the effectiveness and appropriate scale of riparian habitat restoration, are receiving increasing interest (Arthington *et al.* 2010; Overton *et al.* 2014). Fluctuations in the riparian ecotone have been studied at a range of spatial and temporal scales (Lorenz *et al.* 1997; Thorp *et al.* 2006; Larsen *et al.* 2009; Gurnell *et al.* 2012), reflecting different attempts to describe ecological responses to change and intervention. Despite the frequent use of Carabidae as target organisms in such studies (Framenau *et al.* 2002; Van Looy *et al.* 2007; Jahnig *et al.* 2009a; O'Callaghan *et al.* 2013a), there have been few comparisons of possible sampling techniques that might be most appropriate for this group of invertebrates, for example on exposed riverine sediments (ERS). In general, pitfall traps have been among the most widely used techniques, but there has been considerable discussion of their strengths and weaknesses (Andersen 1995; Bates *et al.* 2005; Liu *et al.* 2007; Van Looy *et al.* 2007). Moreover, there is a range of constraints that might affect the choice of sampling technique for this group in particularly dynamic environments.

With ERS specialist Carabidae, it is recommended that sampling should focus on the wetted “activity zone” adjacent to the edge of the water (Bates and Sadler 2005). Sampling here is required to be flexible enough to track fluctuations in water level irrespective of what is defined as ERS habitat (Chapter 2). This zone provides an essential micro-habitat for Carabidae, where relative humidity is higher and surface temperatures lower than elsewhere on ERS, which might otherwise exceed > 40°C (Bates and Sadler 2005). Most subsidies of emerging and stranded aquatic arthropods arrive in this zone to potentially become available to terrestrial predators (Bonn and Helling 1997; Bates and Sadler 2005; Paetzold *et al.* 2005; Paetzold and Tockner 2005; Bates *et al.* 2006; Paetzold *et al.* 2006; Bates *et al.* 2007b). As this activity zone expands and contracts with fluctuating water levels, it is a valuable zone within which to understand ERS specialists’ ecology and to track their distribution, which in turn tracks fluctuating water levels (Bates and Sadler 2005).

The dynamics both of specialist ERS Carabidae and their zone of activity combine to require a flexible sampling technique**.** Rapid, reliable and efficient sample techniques are important in this group where extensive survey area, such as reaches or whole river systems that might contain multiple, separate ERS patches, must be sampled serially and quasi-simultaneously. A sampling technique should also, ideally, provide equal likelihood of recording common and rare species (Dornelas *et al.* 2013), and ensure that taxa are recorded in relation to their true occurrence in the target environment.

Several survey techniques have been used to sample arthropods on ERS, including timed hand searches (Sadler *et al.* 2004; Bates and Sadler 2005; Bates *et al.* 2005; Sadler *et al.* 2006; Henshall *et al.* 2011), pitfall traps (Sadler *et al.* 2004; Bates and Sadler 2005; Bates *et al.* 2005; Bates *et al.* 2007b; Liu *et al.* 2007; Van Looy *et al.* 2007), excavation (Dieterich 1996; Sadler *et al.* 2004; Bates *et al.* 2005; Sadler *et al.* 2006), surveying within quadrats (Andersen 1983a, 1995; Bates and Sadler 2005; Bates *et al.* 2005; Sadler *et al.* 2006) and buried sediment traps (Dieterich 1996; Bates *et al.* 2005). The two most widely used techniques are pitfall traps and, less frequently, hand searches. Pitfall traps sample cursorial species, the rate of movement of which is influenced by environmental conditions (e.g., air temperature). Pitfall traps can be standardised (e.g., trap dimensions, numbers of traps, number of days left out, locations) and the traps can capture high numbers of animals during a relatively short period. Dry pitfall traps can be used but have the disadvantages of animals escaping, within-trap predation, desiccation, drowning (though wet pitfall traps achieve this by design) and within-trap stress (Bates and Sadler 2005). Pitfall traps are also static and are vulnerable to changing weather and river conditions, and to disturbance by livestock.

By contrast, timed hand searches enable the researcher to track a particular habitat feature such as the activity zone (Sadler *et al.* 2006). The technique may also include splashing water over the substrate to force fossorial species to the surface (Bates *et al.* 2005), and turning over stones to expose individuals for capture with an aspirator (Bates *et al.* 2005). By ensuring a standard effort on each sample, data collected on both cursorial and fossorial species using hand searches can be compared.

Within the general context of informing sampling techniques to be used in a more extensive survey, this particular study aimed to compare the efficiency between pitfall traps and timed hand searches to sample the greatest number of specialist ERS Carabidae within assemblages during successive, rapid, spatio-temporal sampling on ERS; testing the hypothesis that there was no difference in representativeness of ERS specialist Carabidae between techniques.

3.2 Methods

3.2.1 Study Area: Selecting the Study Sites

The study area is described in detail in Chapter 1. In outline, the area was selected from a geomorphologically active stretch of the River Usk (*Figure 1.3*), within Management Unit 5 of the River Usk Special Area of Conservation Core Management Plan (CCW 2009). The exact location lay immediately downstream of the River Nant Menascin and several hundred metres upstream of the River Caerfanell, both streams forming part of the River Usk Tributaries Site of Special Scientific Interest (SSSI) and River Usk Special Area of Conservation (SAC), (Ordnance Survey grid references SO31002252 to SO31162243). Within a reach measuring approximately 3.5 km between upstream and downstream points, six separate ERS sites (patches) were selected, ranging in size from 400 to 9,200 m^2 (*Table 3.1*). The length and width of ERS were estimated by metre paces along the shoreline (approximate length), and metre paces perpendicularly away from the edge of the water at each sample location to the up-shore edge of exposed sediment, calculating a mean ERS width from the sum of these. An important requirement was that each site was expected to support repeated survey work during the ensuing years based on site size, accessibility, the extent of exposed sediments, and study logistics.

Sites 1 (the most upstream) and 2 were point bars (on the inside of a meander), Sites 3, 4 and 5 were lateral bars (on one river bank), and Site 6 (the most downstream), was an island bar during periods of high river discharge (*Figure 2.1*), otherwise forming a lateral bar.

3.2.2 Comparison of Survey Techniques

During August 2008, timed hand searches and pitfall trap surveys were completed on Sites 1 and 6, the most upstream and downstream, respectively (*Table 3.1*).

Site number	**Site name**	**8 Fig Grid Ref (SO)**	**Approx ERS length m**	**Mean ERS width (sd) m**	**Approximate ERS area m^2**
1	Pencelli Big Bend	99202522	290	32 (14.91, n = 6)	9280
2	Scethrog Big Bend	10552455	250	35 (15.0, n = 5)	8750
3	Scethrog Ox-bows 1	10662470	60	11 (NA, n = 2)	660
4	Scethrog Ox-bows 2	10772481	50	8 (NA, n = 2)	400
5	The Spinney	10972475	180	18 (7.12, n = 4)	3240
6	Newton Island	11502425	300	14 (13.6, n = 7)	4200

Table 3.1 Locations and approximate dimensions of survey sites on the River Usk SAC, August 2008. For the mean ERS width, “n = ?” refers to the number of hand search sample locations per site. Sites 1 and 6 were used for the comparative assessment of survey techniques.

Pitfall Traps

A series of five and four pitfall trap grids (Van Looy *et al.* 2007) were installed, respectively, on Sites 1 and 6 mid-morning on August 29 2008 (*Figure 3.1*). Each 2 x 2 m grid comprised 9 X 500 ml plastic beakers of 90 mm diameter. Traps were set with their rims level with the smaller, firmer pebbles and shingles beneath the coarser top substrate; hand searches revealed that beetles were active only at this level. A flat stone was placed over the top of each trap to emulate the shade provided by the overlying cobbles that might be preferred by some species (Andersen 1985b). One pitfall grid at Site 1 was set in a patch of 100% ground cover on coarse sand where all nine traps were left open (i.e., with no stone lid) on the expectation that the finer sediments and vegetation would inhibit fossorial behaviour. For similar reasons on Site 6, two traps at Grid Location 2, and all nine traps at each of Grid Locations 3 and 4 were left ‘unlidded’, being set within open, coarse sands rather than beneath cobbles or within shingle.

Traps were emptied 2 days later on 31 August. Trapped beetles were collected into a separate vial for each grid location and non-target arthropods were released. All Carabidae from both techniques were identified using Luff (2007) and with the assistance of Brian Levy at the National Museum Wales, Cardiff. To verify rarity of species sampled, species were compared with the national dataset for specialist Carabidae of ERS (Fowles 2004) and the conservation status of each species, where it existed, was provided by the Biodiversity Information Service for Powys and the Brecon Beacons National Park.

Timed Hand Searches

On 8 and 14 August 2008 at Sites 1 and 6, respectively, standardised timed hand searches of 10 minutes duration were completed at sample locations every 50 m along the shoreline adjacent to the river. Starting at the shoreline within the likely zone of beetle activity and working perpendicularly away from the water's edge for 2 to 3 m, a small hand rake was used to pull aside the surface cobbles, revealing the smaller, damper pebbles and shingle below, where invariably the beetles roamed (*Figure 3.2*). All Carabidae were collected using an aspirator during a ten minute effort at each sample location; all locations were spaced 50 m apart along the water's edge. The exact Ordnance Survey grid co-ordinates were recorded for each sample location. Beetles at each site were collected in a single container containing 9:1 water and ethylene glycol plus ethanol.

Figure 3.1 Sites 1 (above) and 6 (below): position of pitfall traps and hand search sample locations during comparative experiment in 2008 comparing the efficiency of both techniques to sample a representative assemblage of specialist Carabidae of exposed riverine sediments on the River Usk, Wales.

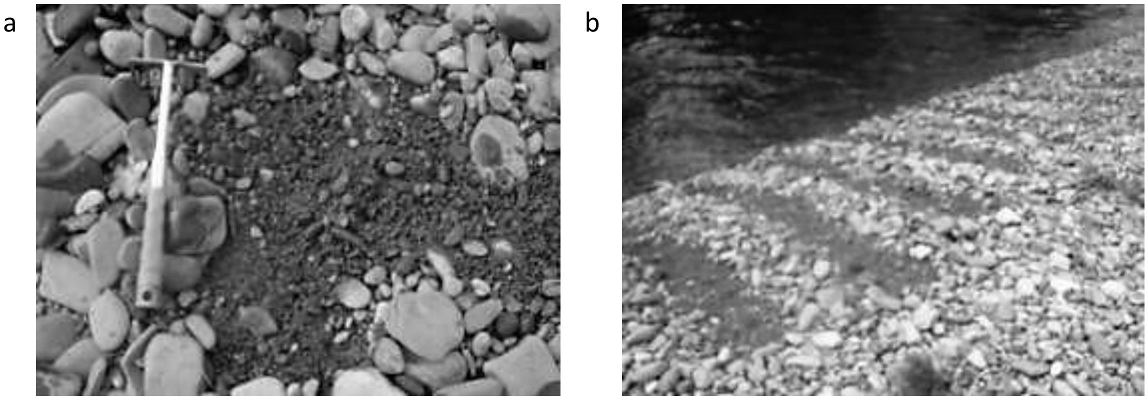


Figure 3.2 Raking technique for timed hand searches. a) Small hand rake used to remove surface cobbles, exposing the finer sediments beneath. b) Using the hand rake, sediments exposed in strips within 2 m to 3 m of the edge of the water.

3.2.3 Extended Assessment of Hand Searches (2009 to 2011)

Eventual incorporation of hand searches into the overall study design allowed a more extended assessment of the quality of data produced over the period 2009 – 2011. Timed hand searches were made at each site and sample location during three sample visits each year in early, mid- and late summer (April/May, June/July, August/September, respectively). Samples were collected separately for each sample location during each visit and otherwise treated as above.

3.2.4 Data Analysis

Comparison between pitfall trap grids

Kruskall-Wallis tests were used to compare the species richness of Carabidae, and separately the ERS specialists, in pitfall traps located wholly within coarser sediments, where they were covered by a flat stone, versus those located within finer sediments and/or ground cover, where they were left 'unlidded'.

Comparison of sampling techniques

Species richness, ERS specialist richness, total beetle abundance, abundances of ERS specialists, mean counts, percentage counts of ERS specialist species collected per technique, Sorensen's Similarity Index and co-efficient of variation were determined for both techniques at the site scale. These variables were then compared between techniques using t-tests, the Kruskall-Wallis test (adjusted for ties) and general linear modelling using site and sampling technique as independent factors; compliance with assumptions of ANOVA was tested beforehand. Co-efficients of variation (CV) were used to evaluate the dispersion within sample data for both sample techniques. Co-efficient of variation is calculated from the ratio of standard deviation of the data to the mean of the data (UCLA 2014). All analyses were completed using Minitab 16®.

As a supplementary check to confirm that the majority of species had been sampled, rarefaction curves were generated to examine whether or not sampled species accumulation reached a species richness asymptote. By this analysis, as more samples are taken, or as more individuals are captured, the encounter rate of new species declines and the steepness of the species accumulation curve levels off (asymptote). Achieving an asymptote indicates that all species have been captured by the technique deployed, with the rarer species occurring in low numbers or as singletons. The fewer the samples taken or individuals sampled within the asymptote, the more effective the sampling technique for the spatial or temporal survey being undertaken.

Interpolated rarefaction curves were produced for both techniques using the EstimateS programme (Colwell *et al.* 2012; Colwell 2013). This provides smooth interpolated rarefaction curves with confidence intervals. EstimateS uses the sample data (the reference sample) and an extrapolation of this (the interpolation), to provide a computed estimate of species richness irrespective of sample size. This technique avoids the comparison of samples based upon the size of the smallest sample, which traditionally has necessitated the ‘disposal’ of the larger dataset (Colwell *et al.* 2012; Dornelas *et al.* 2013). By using this approach, smaller samples can be extrapolated for comparison with larger samples and their associated confidence intervals. A species richness asymptote is generated for each sample irrespective of sample size, as well as a rarefaction or extrapolation plateau that indicates the level of sample effort at which full species richness (species encountered) has been recorded.

Three Year Samples

Using only the data for the first year of timed hand searches in 2009, and to confirm the robustness of the preferred survey technique, a simple rarefaction evaluation was drawn for the log abundance and species richness of ERS specialist species against number of samples.

3.3 Results

3.3.1 Comparison between Pitfall Trap Grids

Using the Kruskall-Wallis test, there was no significant difference in Carabidae species richness sampled between any of the covered or uncovered pitfall trap grids, either for the entire assemblage per grid (H_8 = 10.42, p > 0.1, adjusted for ties) or for the ERS specialists subset (H_8 = 3.82, p > 0.5). On this basis, all pitfall trap data were subsequently pooled to provide site samples for Sites 1 and 6, for comparison with the hand search site samples.

3.3.2 Comparison of Sampling Techniques (2008 Study)

In total, during the 2008 evaluation period, pitfall traps and hand search surveys yielded 220 individuals of 23 Carabidae species. Hand searches sampled almost exactly double the abundance of pitfall traps (143:77). They recorded 12 species, including 6 ERS specialists, while the pitfall traps recorded 15 species, also including 6 ERS specialists; nine specialist species were recorded overall. Although not significant, hand searches returned higher abundance of the genus *Bembidion*, whilst pitfall traps returned higher abundance of non-specialist Carabidae. Of the 23 species recorded, three ERS specialists were Nationally Notable (Nb), *Amara fulva* (Mueller O.F.), *Bembidion monticola* (Sturm) and *Clivina collaris* (Herbst). Additional ERS specialists were *B. atrocaeruleum* (Stephens), *B. decorum* (Zenker in Panker), *B. fluviatile* (Dejean), *B. punctulatum* (Drapiez), *B. prasinum* (Duftschmid) and *B. tibiale* (Duftschmid). *Bembidion atrocaeruleum*, *B. decorum* and *B. prasinum* were the three most numerous species overall, with the nocturnal *C. collaris* the most numerous species only recorded in the pitfall traps. Ten species recorded in 2008 were not encountered during the subsequent three years: *Amara fulva*, *A.aulica* (Panzer), *Agonum marginatum* (Linnaeus), *B. fluviatile*, *B. lampros* (Herbst), *B. stephensii* (Crotch), *Loricera pilicornis* (Fabricius), *Nebria salina* (Fairmaire and Laboulbène), *Pterostichus niger* (Schaller) and *Trechloblemus micros* (Herbst). Ten species found in the hand searches were not encountered in the pitfall traps, of which three, *Bembidion monticola*, *B. prasinum* and *B. tibiale* are ERS specialists. Conversely, eight species sampled in the pitfall traps were not sampled during the hand searches, of which two, *Amara fulva* and *Clivina collaris*, are ERS specialists (Fowles 2004).

Whilst there was no significant difference between techniques for species richness, species richness of ERS specialists, abundance of ERS specialist beetles or abundance between sites, abundances in hand searches were greater (*Table 3.2*). Following approximately 130 minutes of survey by hand searches across the two sites, versus 48 hours of pitfall trapping, timed hand searches yielded over 92% of ERS specialist beetles within catches whilst pitfall traps yielded just under 68% ($F_{1, 5} = 23.93$, $p < 0.05$, R^2 adj' = 80.96%). Across the two survey sites, 60% of the beetles captured in hand searches were ERS specialists by comparison with less than 24% in pitfall traps ($F_{1, 5} = 24.97$, $p < 0.05$, R^2 adj' = 81.55%). Sorensen's Similarity Index indicated that hand searches achieved higher inter-site similarity than pitfall traps, whilst similarity between techniques was lower than inter-site similarity by either technique. For the mean abundance per ERS specialist species ($F_{1, 5} = 11.26$, $p = 0.07$, R^2 adj = 72.91%) and also per ERS specialist species per site ($t = -6.06$, $p < 0.05$, $n = 3$), hand searches captured significantly higher numbers than pitfall traps. Overall, by tallying data from both sites, hand searches provided a lower co-efficient of variation than pitfall traps for mean abundance per ERS specialist species (0.95 versus 1.13), indicating a lower dispersion within the data and therefore a more consistent means of sampling ERS specialists.

Table 3.2 Summary comparison between timed hand searches (HS) and pitfall traps (PF) used to sample Carabidae on two patches of ERS. Significance levels indicate * $p < 0.05$. Shaded boxes indicate no calculation. $^{+}$Mean abundance per sample derived from 6 hand search samples and 5 pitfall samples on Site 1; and 7 hand search samples and 4 pitfall samples Site 6. All samples were pooled prior to analysis.

Data	Sample Size						Statistical technique
	Site 1		Site 6		Between methods		
	HS	PF	HS	PF	HS	PF	
Species richness	11	9	7	13	12	15	GLM (site and technique as independent factors)
Statistical comparison	NS: $F_{2,5} = 1.00$, $p > 0.1$				NS: $F_{1,5} = 1.00$, $p > 0.5$		
Species richness ERS specialists	5	5	5	5	6	6	
Statistical comparison	NA				NA		
Abundance total	95	35	48	42	143	77	
Statistical comparison	NS: $F_{2,5} = 4.06$, $p > 0.1$				NS: $F_{1,5} = 5.32$, $p > 0.1$		
Abundance ERS specialists	86	26	46	26	132	52	
Statistical comparison	NS: $F_{2,5} = 3.45$, $p > 0.1$				NS: $F_{1,5} = 9.14$, $p > 0.05$		
Abundance Bembidioniidae	90	16	47	18	137	34	
Statistical comparison	NS: $F_{2,5} = 2.05$, $p > 0.1$				NS: $F_{1,5} = 10.17$, $p = 0.086$		
Abundance generalist species	9	9	2	16	11	25	
Statistical comparison	NS: $F_{2,5} = 1.65$, $p > 0.1$				NS: $F_{1,5} = 4.0$, $p > 0.1$		
Mean abundance per sample $^{+}$	15.83	7.00	6.86	10.50	11	8.56	
Statistical comparison	NS: $F_{2,5} = 0.19$, $p > 0.5$				NS: $F_{1,5} = 0.5$, $p > 0.5$		
Mean abundance ERS specialist species per sample	14.33	5.20	6.57	6.50	10.15	5.78	
Statistical comparison	NS: $F_{2,5} = 0.51$, $p > 0.5$				NS: $F_{1,5} = 2.99$, $p > 0.1$		
Proportion of ERS specialist beetles per technique	90.53%	74.29%	95.83%	61.90%	92.31%	67.53%	
Statistical comparison	NS: $F_{2,5} = 0.17$, $p > 0.5$				*		
Proportion of ERS specialist species per site	66.15%	20.00%	51.00%	28.89%	60.00%	23.64%	
Statistical comparison	NS: $F_{2,5} = 0.07$, $p > 0.5$				*		
Sorensen's Similarity Index	Hand searches = 0.96 Pitfall traps = 0.87				Both techniques = 0.76		
Abundance per species comparison between techniques					NS: $H_1 = 0.26$, $p > 0.5$ (adj for ties)		Kruskall-Wallis (adj' for ties)
Mean abundance per species	5.59	2.06	2.82	2.47	6.22	3.35	GLM (site and technique as independent factors)
Statistical comparison	NS: $F_{2,5} = 1.63$, $p > 0.1$				NS: $F_{1,5} = 5.39$, $p > 0.1$		
Mean abundance per ERS specialist species	17.2	5.20	9.20	5.20	22.00	8.67	
Statistical comparison	NS: $F_{2,5} = 2.6$, $p > 0.1$				$p = 0.079$		
Mean abundance per species per site	7.65		5.29		9.57		2-tailed, 1 sample t-test
Statistical comparison	NS: $t = 0.41$, $p > 0.5$, $n = 3$						
Mean abundance per ERS specialist species per site	16.00		9.00		20.44		
Statistical comparison	*						
Differentiation by techniques between sites					NS: $H_1 = 1.59$, $p > 0.2$	NS: $H_1 = 0.51$, $p > 0.4$	Kruskall-Wallis (adj' for ties)
Mean abundance per species :coefficient of variation	1.90	1.59	2.52	1.48	2.22	1.78	
Mean abundance per ERS specialist sp: coefficient of variation	0.84	0.86	1.24	1.06	0.95	1.13	

3.3.3 Species Accumulation (Rarefaction)

Species accretion rate for pitfall traps was higher than for the hand searches (*Figure 3.3*). The asymptote for hand searches occurred at lower beetle abundances within the samples than for pitfall traps. Extrapolation of the estimated richness showed that the standard deviation for pitfall traps converged towards hand searches beyond the reference point for the original samples (*Figure 3.3*), illustrating that whilst pitfall traps achieved a 'faster' accumulation of species per beetles sampled, both techniques converged towards equilibrium as maximum species accumulation was achieved. This demonstrated that, eventually, both techniques provided a reliable representation of ERS specialist beetles. However, the faster accretion rate for pitfall traps reflected the higher number of non-specialist species trapped, whilst still sampling a weaker representation by proportion of ERS specialist beetles than hand searches (*Table 3.2*).

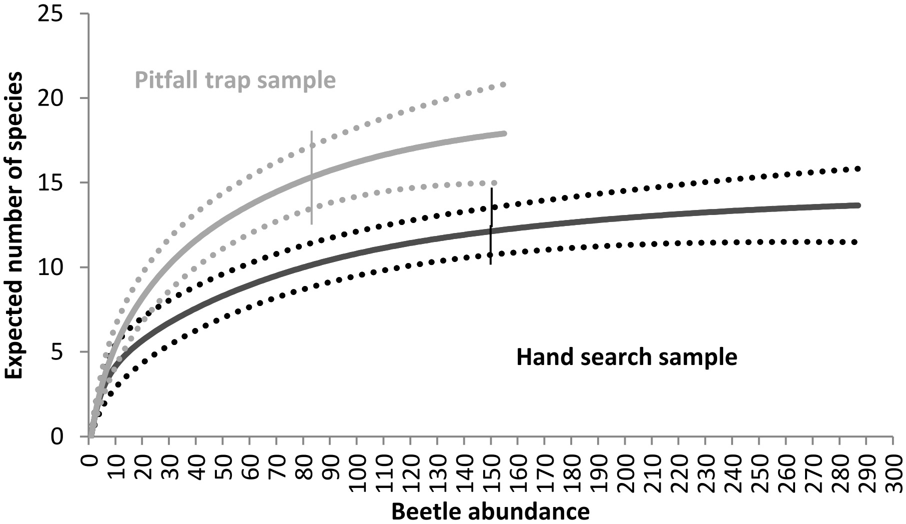


Figure 3.3 Interpolated species accumulation curves and modelled standard deviations (dashed lines), comparing both survey techniques on combined data for Sites 1 and 6 during 2008. Vertical lines indicate the sample size for each technique. Using the EstimateS package (Colwell 2013),

3.3.4 Using Hand Searches during Three Year Surveys

During 2009 - 2011, timed hand searches were completed on three sampling visits each year to 27 sample locations spread across six sample sites. A total of 4,393 beetles was captured and identified, with all individuals identified to 28 species. This involved a total of 90 hours field survey effort plus the time required to identify each beetle. All larvae sampled were grouped as a generic "larvae" rather than identified to species. Twelve species recorded during the three consecutive sampling years, were not recorded during the initial comparison study. Of these, three were ERS specialists, *B. dentellum* (Thunberg), *B. lunatum* (Duftschmid) and *Chlaenius vestitus* (Paykull)**.** The other nine species were: *Amara aenea* (De Geer), *Agonum lugens* (Duftschmid), *B. guttala* (Fabricius), *B. properans* (Stephens), *Bracteon littorale* (Oliver), *Nebria brevicollis* (Fabricius), *Patrobus atrorufus* (Ström), *Platynus assimilis* (Paykull), *Pterostichus nigrita* (Paykull) and *P. vernalis* (Panzer).

3.3.5 Species Accumulation (Rarefaction) during Three Years

Using only the data for 2009, an asymptote for species richness of ERS specialists was achieved during the first year of hand searches, where 10 of the 12 specialist species recorded over three years, were recorded within the first eight samples (*Figure 3.4*). The two further ERS specialists were *B. lunatum*, recorded at Site 6 during 2010, and *Chlaenius vestitus*, recorded at Site 5 during 2011. Thus, within 80 minutes (eight samples), 85% of ERS specialist species had been recorded by hand searches within 1.5% of the total survey time (90 hours or 5,400 minutes). Expressed another way, of the 277 samples taken during three years, 85% of ERS specialist species had been recorded within 2.9% of samples.

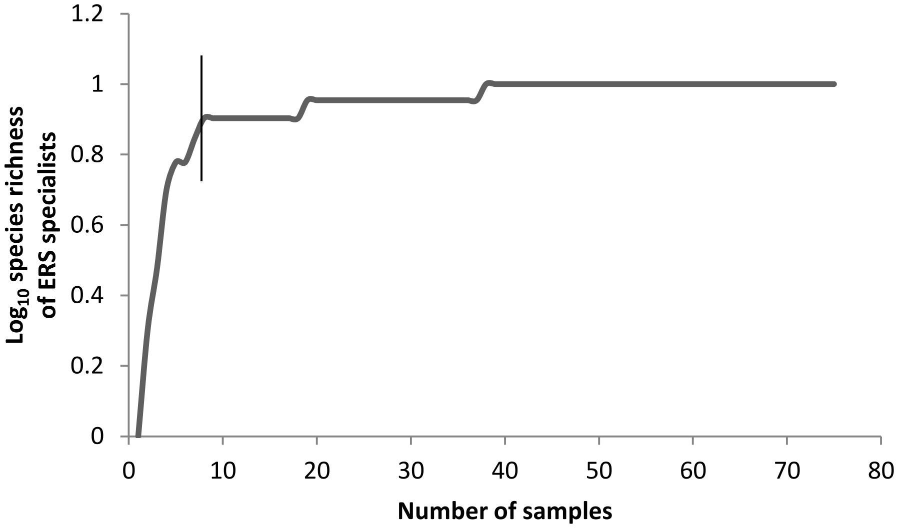


Figure 3.4 Log_{10} species richness accumulation for ERS specialist Carabidae recorded from six ERS sites on the River Usk during 2009, following three sample visits to 75 sample locations. The vertical line indicates eight samples.

3.4 Discussion

Whereas this study hypothesised that there was no difference in representativeness of ERS specialist Carabidae between timed hand searches and dry pitfall traps, the former proved to be the more representative and robust technique. Whilst there was no significant variation in species richness or abundance of ERS specialist species, timed hand searches provided higher numbers than pitfall traps for these variables. They also provided a significantly higher proportion of ERS specialist species and abundance thereof. Timed hand searches made a stronger distinction between sites by proportion of ERS specialists, sampled a higher mean abundance per ERS specialist species and achieved higher inter-site assemblage similarity than pitfall traps. During a three year survey, timed hand searches had sampled ten of the 12 species of ERS specialists recorded throughout the period within the first eight sample locations during the first year, of which there were 75 during the first year and 277 during three years; and during the first 80 minutes of a 90 hour sampling season. This demonstrated that, in order to achieve a presence-absence understanding of ERS, for which pitfall traps have traditionally been used (Bates and Sadler 2005), timed hand searches achieved this within a matter of hours, whereas pitfall traps might only achieve this within days. Achieving a rapid asymptote for specialist species also demonstrated the naturally low species richness of this environment (Sadler *et al.* 2006). Timed hand searches were, therefore, a more robust, reliable and representative technique than pitfall traps for sampling ERS specialists within both a spatially and temporally dynamic activity zone, and recording taxa in relation to their true occurrence in the target environment.

Additionally, though not significant, hand searches caught more species of Bembidioniidae than pitfall traps. *Bembidion* species are active fliers (Luff 2007), which is likely to be a diurnal activity. Hand searching may, therefore, be more effective for sampling this genus by revealing the location of individuals rather than relying upon the chance intersection of beetle behaviour and pitfall traps. By contrast, the traps sampled a higher number and proportion of non-specialist species, were vulnerable to disturbance and were not well suited to rapid re-deployment within the activity zone.

By testing two sampling techniques, the study determined that hand searches were more reliable and rapid for sampling beetles on repeated occasions across a range of sites and to generate data representative of dynamic ERS. The technique proved to be robust by being representative and reliable: searching within a defined sample zone for a set duration at each sample location, standardising the samples and permitting comparisons between them (Dornelas *et al.* 2013). The data on beetle abundance and species richness obtained from hand searches were more representative of specialist ERS assemblages (Fowles 2004) than data collected from pitfall traps. However, comparable studies examining the suitability of different sampling regimes on Carabidae in other habitats are lacking in the literature, so it is unclear if these results are mirrored elsewhere.

Species accretion was higher in pitfall traps, indicating a higher, early accumulation of generalist Carabidae, underlining that pitfall traps are a more generalist and less targeted survey technique. They present several known disadvantages including, possibly the most obvious, that they are vulnerable to disturbance by livestock (Bates *et al.* 2007a)! In this study, they were left *in situ* following the first visit but an intended second visit proved fruitless with the traps destroyed (kicked over or sediment-filled) by passing sheep. They are also prone to inundation or being washed away during a flood in the riparian zone. Pitfall traps over-represent larger carabid species by number and abundance (Andersen 1995), which was demonstrated by the higher number of generalist species sampled. This cannot be accounted for by diurnal rhythms or life cycle stages alone and may be an artefact of beetle behaviour. Pitfall traps are more efficient at trapping adults than larvae (Andersen 1995) but require higher unit effort to track shifting habitat zones such as the activity zone for ERS specialists adjacent to the water's edge. Owing to the skewed distribution of species sampled, pitfall traps are also inappropriate for studying dominance ratios, species ecological niches and ecological diversity, despite being known to record higher ecological diversity than quadrats or light sampling (Andersen 1995; Liu *et al.* 2007). Pitfall traps proved helpful in sampling additional ERS specialists but provided no other significant advantage over hand searches. On this evidence, they are less useful for rapid surveys carried out on a repeated basis over a number of years on ERS.

This study confirmed that standardised hand searches are a suitable approach for prolonged, high resolution biodiversity studies over varying scales that are lacking in the literature (Dornelas *et al.* 2013). Using a small hand rake was particularly effective, requiring minimal prior preparation and enabling rapid and even turnover of overlying cobbles in repeated rows to a standardised depth in the sediments, revealing the smaller and damper (and likely cooler) lower sediments where the beetles were found. The hand rake provided the combined benefits of partial excavation, rapid and even-handed turning over the surface stones, as well as exposing both cursorial and potentially fossorial species. Hand searches rely upon suitable weather conditions during which the target fauna are active, and the skills of the surveyor (Bates *et al.* 2005). In most cases, it is not a wholly quantitative technique but as was demonstrated by this study, can be standardised and, importantly for a large survey area, is relatively rapid. The technique avoids the inherently qualitative factor of turning over stones by hand (Bates and Sadler 2005), though it was not designed to collect every beetle present, only to sample presence and abundance in a measured, repeatable way in space and time. It also ensured that beetles were sampled from approximately the same distance to the surface. No account was made in the initial comparative or the three year study of the varying depths at which different fossorial species might occur; some species were assumed therefore to have been overlooked. Detail on the depth at which different species reside is, however, missing in the literature.

Habitat features of classically defined ERS include naturally deposited sands, gravels, shingle and cobbles between the high water level and typical river base flow (Bates *et al.* 2005). This definition excludes additional habitat features such as riverbeds that are exposed during periods of prolonged low flow. By sampling within the activity zone close to the water's edge, during a three year period of repeated low river discharge stability (Chapter 4), this study demonstrated that during such an event it is appropriate to include all exposed sediments connected directly to the ERS at the time of study; failure to do so might exclude significant faunal adaptation to a modified environment. This potentially widens the survey area and alters the range within which a meta-assemblage disperses.

This emphasises the need for a rapid and reliable survey technique to cover such variability and to represent faunal behavioural adaptations.

The variation in species recorded during the comparative study but not during the subsequent three years, and *vice versa,* might either have indicated ecological succession between years or was illustrative of the elusiveness of the fauna within any rapid sampling process. It might also have been attributable to the late summer increase in taxa (Armitage *et al.* 2001) during the comparative experiment and the disappearing likelihood of encountering additional species each year (large scale temporal rarefaction).

4 Influences on the Distribution of Carabidae (Coleoptera) on Exposed Riverine Sediments

Summary

Rivers are among the most threatened ecosystems globally, and the riparian zone is especially vulnerable to the combined effects of land use, discharge regulation and climate change. This chapter investigated how the distribution and abundance of one particular insect group, the specialist carabid beetles of exposed riverine sediments (ERS), might reveal wider ecological influences on this ecotonal environment. Using three seasonal hand collections in the early, mid- and late summer during a three year period of persistent low river discharge (2009-2011), carabids were studied at six sites along the River Usk Special Area of Conservation, Wales. Species and assemblage patterns were related to environmental data using principal components analysis, the Kruskall-Wallis statistic and general linear modelling. River discharge during the study years was compared to the previous twelve years using general linear modelling.

A total of 4393 beetles of 28 species were collected, including 11 ERS specialist Carabidae. Four species, *Bembidion atrocaeruleum*, *B. prasinum*, *B. decorum* and *B. punctulatum*, dominated carabid assemblages among which *B. prasinum* favoured more exposed locations closer to the shoreline while *Bembidion atrocaeruleum* was more ubiquitous. Annual summer river discharge during the study was among the lowest throughout the preceding twelve years, and the abundance of *B. atrocaeruleum* declined linearly among years whilst the other three species increased. Whilst there may be a life cycle effect, this suggested a decline in conditions favourable to ERS specialists but amelioration for species close to the recently exposed shoreline. Despite significant inter-annual variation in habitat conditions and ground cover encroachment, GLM suggested reach- or catchment-scale variations through time and between sites affected ERS assemblages more than local habitat variability.

These data illustrate how several ERS Carabidae responded differentially to discharge fluctuations between sites and years, and how management at the catchment scale might be more likely to achieve favourable conservation outcomes than at the reach or site scale. The data also illustrate how this specialist group of ERS organisms might be affected by ‘riparian squeeze’ between land use encroachment and river regulation, and how ERS and specialist Carabidae might be used as sentinels to record the effectiveness of management intervention within the catchment.

Key words: Beetles, *Bembidion*, Invertebrates, Riparian Zone, Regulation, River Usk, Sentinel.

4.1 Introduction

Increasingly, river systems are emphasised as hotspots for both biodiversity and anthropogenic activities that are driving extinction faster than in most other ecosystems, for example through pollution, water and gravel abstraction, canalisation and discharge regulation (Paetzold *et al.* 2008; Strayer and Findlay 2010; Vaughan and Ormerod 2012). Management or policy actions that might arrest this loss and conserve riverine biodiversity, for example by achieving Favourable Conservation Status (EC 1992) and Good Ecological Status (EC 2000), require greater understanding of impairment processes and opportunities for restoration (Jahnig *et al.* 2009b).

While much of the conservation emphasis in river systems has focussed on the wetted river channel, species and habitats in the riparian zone are also at risk from processes including river regulation, land use encroachment and channel engineering (Ballinger and Lake 2006; Jonsson *et al.* 2012; Jonsson *et al.* 2013). For example, exposed riverine sediments (ERS) are important habitats that depend on geomorphological dynamics in the riparian zone, but their distribution and extent has declined (Bates *et al.* 2009; Andersen 2011b; Baiocchi *et al.* 2012; O'Callaghan *et al.* 2013b). In similar environments elsewhere, river discharge reduction has led to a decline in diversity and abundance of ground-dwelling arthropods typical of these riparian zones (Greenwood and McIntosh 2010; McCluney and Sabo 2012). Furthermore, in the absence of managed adaptation, riparian habitats are vulnerable to the adverse effects of climate change owing to high levels of exposure to discharge fluctuation and habitat modification (Capon *et al.* 2013).

In addition to their susceptibility to change, exposed riverine sediments are interesting environments in which to examine the effects of habitat perturbation on faunal distribution. This is because of the regular switch between inundation and exposure (Bates *et al.* 2006), the fluctuating interaction between aquatic and terrestrial habitats and species found there (Henshall *et al.* 2011), their occupancy by specialist organisms such as Carabidae (Coleoptera) (Bates *et al.* 2009; O'Callaghan *et al.* 2013b), and the response of such organisms to environmental change (Bates and Sadler 2005; Bates *et al.* 2007b; Kleinwaechter and Rickfelder 2007; Van Looy *et al.* 2007). While the environmental conditions required for ERS-dependent specialist Carabidae have been described (Bates and Sadler 2005; Sadler *et al.* 2006), the exact factors affecting riparian species distribution are not fully understood (Thorp *et al.* 2006). Similarly, while the effects of flood frequency on the stabilisation and succession of ERS, and between the rates of disturbance and associated species richness and diversity, have been described (Bornette and Amoros 1996; Amoros and Bornette 2002; Van Looy *et al.* 2005; Bates *et al.* 2006; Bates *et al.* 2007b; Rolls *et al.* 2012), there are fewer data illustrating how ERS assemblages vary during prolonged periods of stable or falling discharge. The effects of discharge patterns are likely to be particularly important in the wetted zone within a few metres of the river's wetted perimeter as this provides an activity zone where ERS specialists assemble in higher densities (Bates and Sadler 2005; Bates *et al.* 2005; Sadler *et al.* 2006; Bates *et al.* 2007b; Paetzold *et al.* 2008).

In this chapter the distribution and abundance of carabid beetles on ERS in the catchment of the River Usk, Wales (UK), are examined over a three year period, during which annual river discharge declined year-on-year and no inundation events occurred. The study tested the hypothesis that local habitat character had larger effects on carabid assemblages than variations within and between years. The distribution of Carabidae close to the water's edge was examined in relation to a range of within-patch habitat variables as well as inter-patch and inter-annual change.

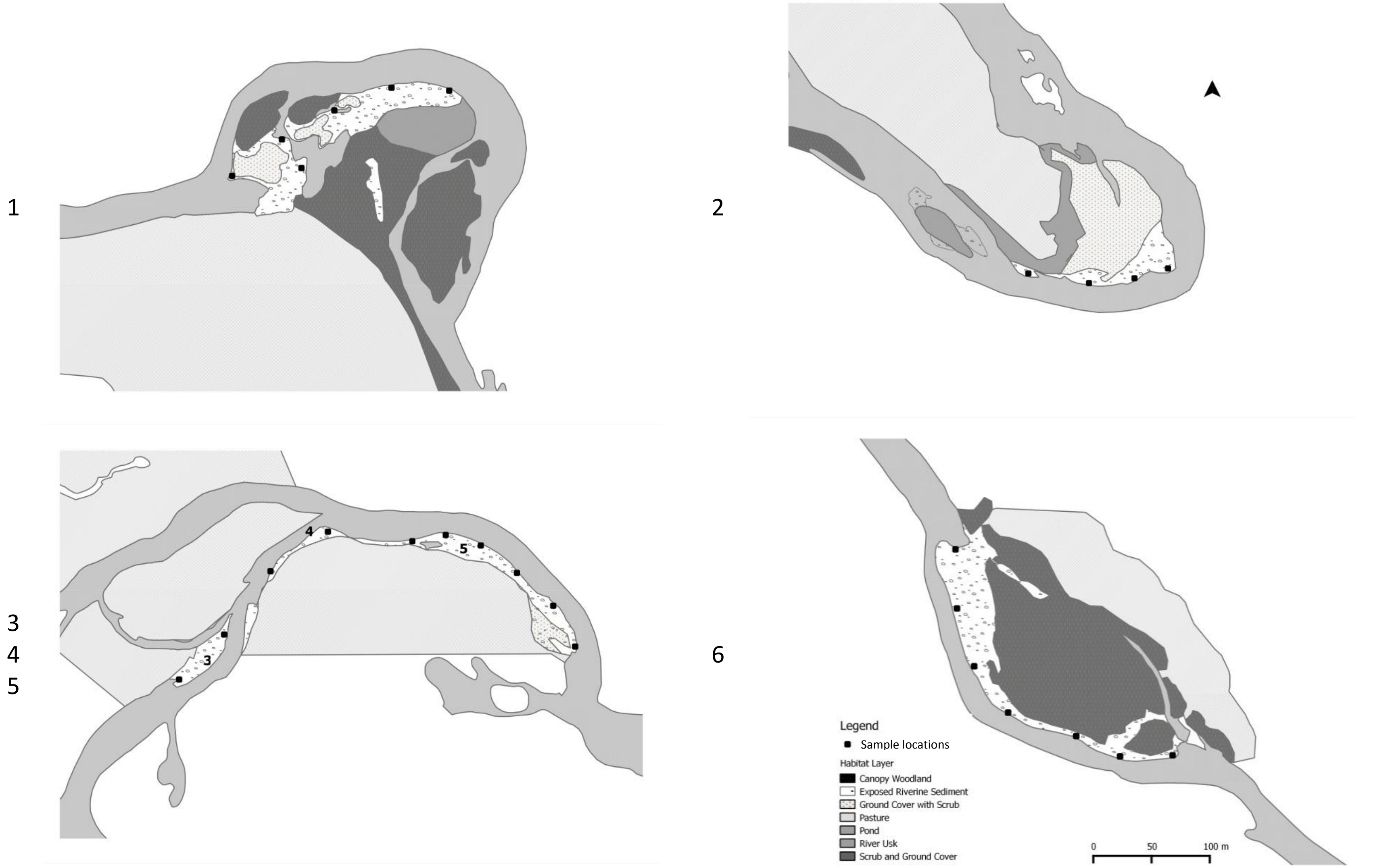


Figure 4.1 Location of ERS study sites 1 – 6 on the River Usk Special Area of Conservation, illustrating the approximate distribution of exposed sediments and recorded habitat features during three years 2009 to 2011.

4.2 Methods

4.2.1 Study Area: Selecting the Study Sites

The study area (*Figure 4.1*), described in detail in Chapter 1, was selected from within Management Unit 5 of the River Usk Special Area of Conservation (SAC) Core Management Plan (CCW 2009). It lay immediately downstream of the Nant Menascin and several hundred metres upstream of the Caerfanell, both streams forming part of the River Usk Tributaries Site of Special Scientific Interest (SSSI) and River Usk SAC. Each of the chosen areas of ERS, formed of point or side bars of exposed, deposited bed material, was inspected visually either from the same bank or opposite bank for its likely suitability to support repeated survey work over three years. Suitability was based upon likely extent of exposure, accessibility and logistics. Six sites were considered suitable for study and ranged in area from c 600 to 14500 m^2.

4.2.2 Habitat Variables

Data for daily river discharge on the River Usk throughout 2000 to 2012 were obtained from the National River Flow Archive, using records from the closest available source at the Llandetty gauging station 4 km downstream of the survey area at SO126203. This allowed an assessment of conditions during the beetle surveys relative to antecedent conditions.

For each site, ERS dimensions (length, width and area of exposed sediment, m and m^2) were estimated by metre paces at the start of each survey season. At each 50 m sample location corresponding to locations where beetles were collected (Section 2.3), habitat variables were recorded based upon methodologies established in previous studies (Bates *et al.* 2005; Bates *et al.* 2006; Sadler *et al.* 2006). These were the percentage of site area occupied by bare exposed sediment, ground cover, scrub and canopy overhanging each 50 m sample location. The physical profile at each location was estimated using the percentage of site area occupied by flat (low angle, low-lying ERS approximating 0^o to 5^o), gentle (more elevated angles approximating 5^o to 15^o, without avalanches at the bar edge) and steep sediment slopes (avalanche faces present, obviously steeper break of slope) within 50 m. The topographic variation of each site was estimated for the percentage of site area occupied by “simple” topography if there was no obvious break of slope within a uniformly flat area, “humped” if there were clear mounds or breaks in slope, and “complex” if there was a combination of slopes, humps, backwaters and flatter areas (Sadler *et al.* 2006). Ordnance Survey grid references were recorded (± 6 m) for an approximate centroid at each sample location using a Garmin Etrex 12 Channel geographic positioning system (GPS). Habitat heterogeneity at each site was categorised from 1-5 (representing low to high heterogeneity) using a matrix devised from the preceding environmental data (*Table 4.1*).

4.2.3 Beetle Sampling and Collection

During the summers of 2009 to 2011, using a small hand rake to move aside the top cobbles and expose the finer sediments below, where invariably the Carabidae lived (*pers. obs*’), all Carabidae spotted were collected using an aspirator at each 50 m along the shore line within the activity zone (Chapter 2). Samples were taken perpendicularly within 2 m to 3 m of the water’s edge during a 10 minute period at each sample location (*Figure 3.2*, and *Figure 4.1*). Sample visits were made on three occasions each year during early, mid- and late summer (April/May, June/July and August/September), at approximately the same locations on each occasion. Each 50 m sample was collected and labelled separately. All beetles were identified to species wherever possible (Luff 2007).

Table 4.1 Matrix to assign habitat heterogeneity on ERS within the River Usk study area; a score of 1 indicates lower heterogeneity than a score of 5.

Habitat heterogeneity score		Uniformly flat	Bare	Some ground vegetation	More than 1 sediment size	Scrub and/or trees	Pools or backwaters	Breaks of slope	Eroding banks/ river cliffs
1 (low)	**At least 2 of:**	✓	✓	✓					
2	**At least 2 of:**		✓	✓	✓				
3	**At least 4 of:**		✓	✓	✓	✓	✓		
4	**All of:**		✓	✓	✓	✓	✓	✓	
5 (high)	**All of:**		✓	✓	✓	✓	✓	✓	✓

4.2.4 Statistical analysis

River Discharge Data

Daily river discharge data, which were provided as 15 minute flows per day each month of each year, were summarised to provide monthly mean discharge per year between 2000 and 2012. Inter-annual and seasonal variation was investigated using general linear models, using year and month as independent factors, comparing annual variations, winter:summer variations and survey season flows (April to September).

Beetle and Habitat Data

Data on the distribution and abundance of beetles, species richness and habitat variables were summarised by year and sample location within sites, pooling abundance per species for each sample location. Variations in beetle assemblage composition among sample locations and times were assessed using ordination methods after initial data assessment to select the most appropriate method. Non-Metric Multi-dimensional scaling and Detrended Correspondence Analysis (DCA) were explored but indicated only modest variations in assemblage composition among samples. For example, DCA indicated less than 25% turnover in species composition along the first ordination axis. Instead, most patterns reflected variations in abundance of a small number of abundant species varying rectilinearly rather than unimodally. Under these circumstances, Lepš (2003) recommended the use of Principal Components Analysis (PCA) for ordination. Data on assemblage composition and abundance for the three years were therefore ordinated using PCA on the correlation matrix to provide major variates that represented the entire beetle assemblage, including rarities and singletons. Habitat data were similarly ordinated using PCA to provide variates that summarised habitat characteristics across years and sample locations.

Species distribution variation for principal species was examined using the Kruskall-Wallis statistic. Inter-annual variations in PCA variates describing habitat factors were investigated using general linear models. Principal component variates describing species composition across samples were related to principal habitat variates, as well as year and site, using general linear models, treating year and site as independent factors and principal habitat variables as sequential covariates, also as independent factors. Species richness, beetle abundance, abundance of four dominant ERS specialists and species principal components were dependent variables. The best fitting models explaining species responses were identified using Akaike's Information Criterion (AIC), given by the equation

$$n * \ln(\sigma^2) + 2(k + 1),$$

where n is sample size, k is the number of variables modelled and σ^2 is the variance calculated from the Adjusted Sum of Squares/n. The lowest AIC value indicated the best fitting model.

Any species occurring in less than 5% of samples was excluded from analyses in order to minimise chance associations. Species abundance analyses were carried out on data transformed by log(n + 2) to normalise distributions. Alternative ordination approaches were undertaken using R (RDCT 2008), whilst all statistical analyses for this study were completed using Minitab 16®; with Akaike's Information Criterion calculations completed in Excel.

4.3 Results

4.3.1 River Discharge

General linear modelling of mean monthly river discharge between 2000 and 2012 highlighted modest variations among years ($F_{12,\ 155} = 1.93$, $p < 0.05$) but far stronger variations between winter and summer discharge ($F_{11,\ 155} = 10.29$, $p < 0.001$, (R^2 adj' = 42.46%), *Figure 4.2a* and *b*). This pattern was maintained during the 2009-2011 survey period ($F_{11,\ 35} = 3.59$, $p < 0.01$, (R^2 adj' = 50.06%), when annual summer discharge (April to September) declined successively to some of the lowest values of the entire 12 year period ($F_{12,\ 77} = 1.73$, $p = 0.08$, R^2 adj' = 11.57%, *Figure 4.2c* and *d*).

4.3.2 Beetle Distribution Patterns

A total of 4393 beetles was recorded over the period 2009-11, with 27 distinct species and 11 ERS specialists identified (Fowles 2004). Larvae were not identified to species and were instead grouped as a single quasi-species "larvae", and treated as an ERS specialist species. Seventeen species, over half of all recorded species, occurred in less than 5% of samples (*Table 4.2*), including four ERS specialists that occurred in low numbers or as singletons. The four most abundant and frequently occurring species, also ERS specialists, collectively contributed 89%, 77% and 86% of total abundance each year. One species alone, *Bembidion atrocaeruleum* (Stephens), contributed just less than 50% of all beetles recorded throughout the three years. This species and the second most abundant, *B. prasinum* (Duftschmid) differed numerically in spatial distribution, with the latter favouring predominantly upstream locations within and between sites, and the former predominantly downstream locations (*Figure 4.3 b* and *c*); however, this pattern was not statistically significant ($H_1 = 2.8$, $p > 0.1$, and $H_1 = 0.01$, $p > 0.5$ for upstream versus downstream sites and sample locations, respectively). *Bembidion atrocaeruleum, B. prasinum* and *B. decorum* (Zenker in Panzer) all peaked in abundance during mid-summer (*Figure 4.3d*), while *B. punctulatum* (Drapiez) peaked during early summer. There was also some contrast in abundance between years, with *B. atrocaeruleum* declining between 2009 and 2011 ($H_2 = 27.13$, $p < 0.001$), while the three other common *Bembidium* species, *B. prasinum*, *B. decorum* and *B. punctulatum* increased ($H_2 = 4.97$, $p = 0.08$, $H_2 = 11.65$, p <

0.01 and $H_2 = 3.1$, $p > 0.1$ respectively; *Figure 4.3a*). Eleven species were used in multivariate analyses, of which seven, including "larvae," were ERS specialists. Seventeen species (of which four were ERS specialists) occurring in less than 5% of samples, were removed from analyses (*Table 4.2*).

Principal components analysis on the species data revealed three components (*Table 4.*3, *Figure 4.*4) that explained 47.3% of the spatio-temporal variation in beetle assemblage composition among samples. Six species increased in abundance along the first PC, including four ERS specialists, *B. atrocaeruleum*, *B. decorum*, *B. monticola* (Sturm) and *B. tibiale* (Duftschmid), and two riparian generalists, *B. tetracolum* (Say) and *Paranchus albipes* (Fabricius). On the second component, three of the same ERS specialists increased in abundance, plus *B. prasinum*; and on the third component two ERS specialists *B. prasinum* and *B. punctulatum* increased along with the generalists, *B. tetracolum* and *Agonum muelleri* (Herbst) (Table 4.3).

4.3.3 Variations in ERS Habitat

Principal components analysis of the habitat variables revealed three major sources of variation across the study area, explaining 60.2% of the spatio-temporal habitat variation (*Table 4.4*, *Figure 4.5*): PC1 reflected increasing site area, shore length, heterogeneity and a shift from flat to gently sloping sediments; PC2 reflected a trend from bare ground to vegetated cover on sloping and humped topography; while PC3 dominantly reflected a shift from steep or sloping, bare sediments to flatter ground (i.e., areas exposed by retreating river discharge over which vegetation might colonise during low flow). Viewed on these axes, Sites 1 and 6 were characterised by their larger size, flatter profile and heterogeneity; Sites 3 and 4 were smaller with most bare ground; Site 5 varied most in vegetation cover, while Site 2 varied most in size of exposure under a combination of different discharge conditions and encroaching vegetation (*Figure 4.5b* (and *Appendix 2*)).

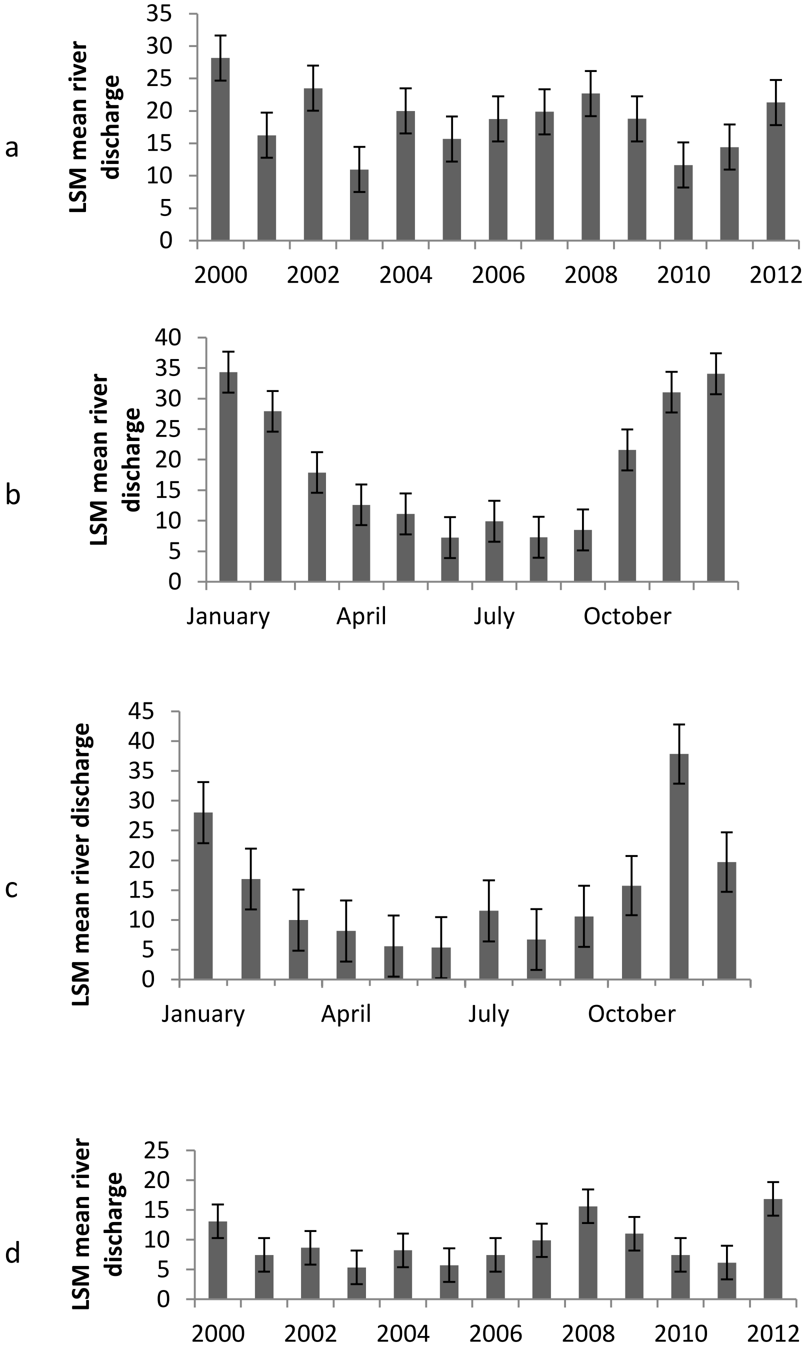


Figure 4.2 Mean discharge (cumecs) (least squares means) and standard error in the River Usk at Llandetty, SO126203, for 2000 to 2012. a) Annual river discharge 2000 to 2012; b) winter and summer months 2000 to 2012; c) summer and winter monthly river discharge 2009 to 2011; and d) summer each year (April to September) 2000 to 2012.

Table 4.2 The abundances of beetle species recorded during a three year study of exposed riverine sediments in the Usk river system, Wales, a) identifying the species used in multivariate analyses and b) those excluded because they occurred in < 5% of samples.

	a	**b**	**2009**	**2010**	**2011**	**Abundance**	**No. samples present**	**ERS specialist?**
1.	*Bembidion atrocaeruleum*		✓	✓	✓	2185	91	✓
2.	*B.prasinum*		✓	✓	✓	589	59	✓
3.	*B.punctulatum*		✓	✓	✓	530	80	✓
4.	*B.decorum*		✓	✓	✓	420	83	✓
5.	*Paranchus albipes*		✓	✓	✓	205	65	
6.	*B.tetracolum*		✓	✓	✓	195	59	
7.	*Agonum muelleri*		✓	✓	✓	84	38	
8.	Larvae		✓	✓	✓	59	30	✓
9.	*B.tibiale*		✓	✓	✓	38	22	✓
10.	*B.monticola*		✓	✓	✓	29	16	✓
11.		*B.lunatum*		✓		10	5	✓
12.		*Bracteon littorale*	✓			10	1	
13.	*Nebria brevicollis*			✓	✓	8	7	
14.		*Clivina collaris*	✓		✓	6	3	✓
15.		*A.lugens*		✓	✓	4	4	
16.		*Platynus assimilis*	✓	✓	✓	3	3	
17.		*Pterostichus nigrita*		✓	✓	3	3	
18.		*Amara sp.*		✓		2	2	
19.		*B.guttala*	✓			2	1	
20.		*B.properans*			✓	2	2	
21.		*Chlaenius vestitus*			✓	2	2	✓
22.		*Amara aenea*		✓		1	1	
23.		*B.dentellum*	✓			1	1	✓
24.		*Harpalus rufipes*		✓		1	1	
25.		*Patrobus atrorufus*			✓	1	1	
26.		*Pterostichus melanarius*	✓			1	1	
27.		*Pterostichus vernalis*		✓		1	1	
28.		*Trechus quadristriatus*			✓	1	1	
		TOTAL	16	19	19	4393		11

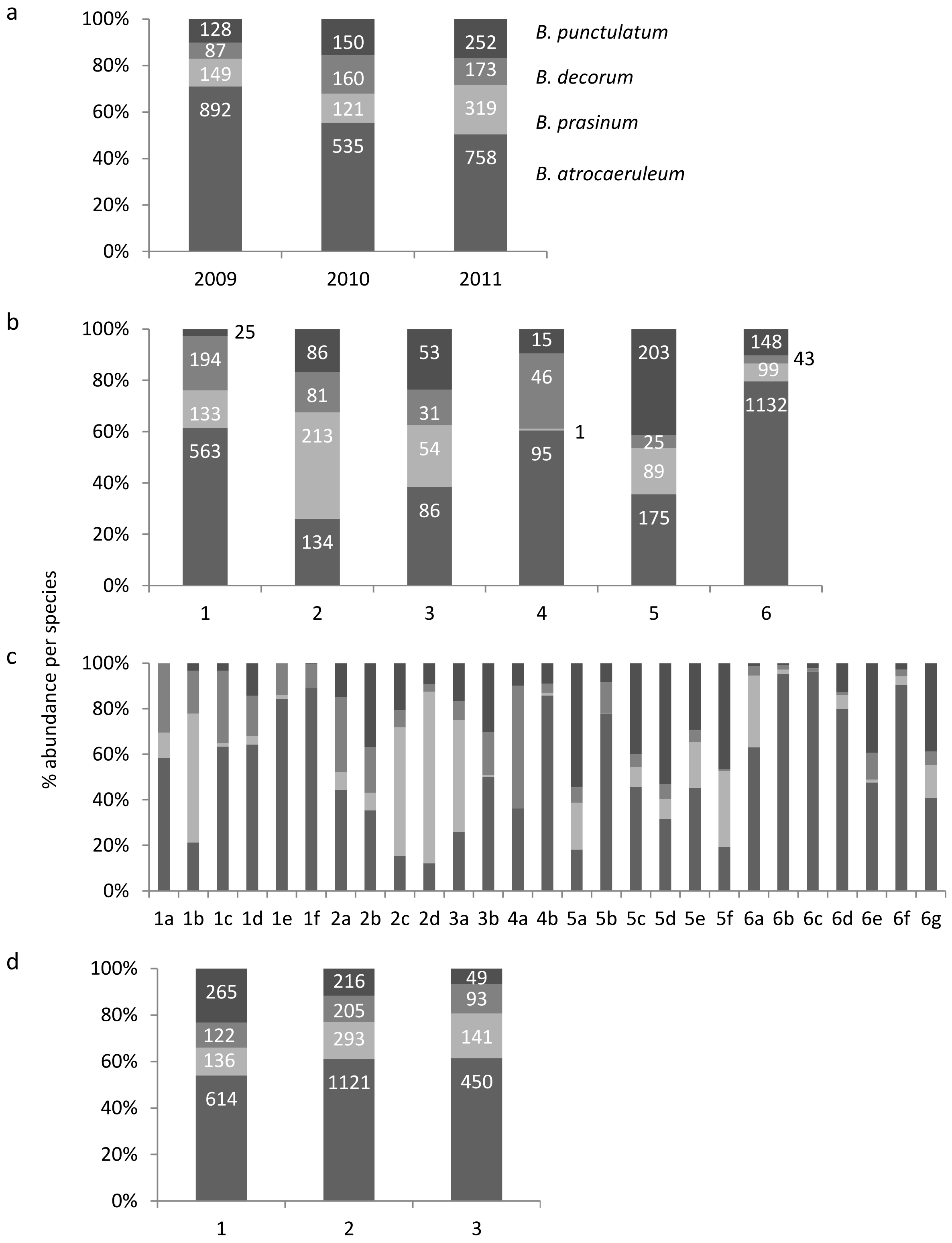


Figure 4.3 Contribution of four principal species to beetle assemblages on 6 ERS sites in the River Usk, 2009-2011: a) each year; b) each site; c) each sample location; and d) each sample visit (1: early summer, 2: mid-summer, 3: late summer). Numbers in the columns provide totals per species. ■ *Bembidion atrocaeruleum*, ■ *B. prasinum*, ■ *B. decorum*, ■ *B. punctulatum*.

Table 4.3 Loading values of dominant beetle species (shaded) on three principal components derived from correlation among their abundances (see *Figure 4.4* for graphical display). ✓ indicates ERS specialist.

	PC1	**PC2**	**PC3**
Eigenvalues	**2.26**	**1.55**	**1.39**
Cumulative proportion	**20.60%**	**34.60%**	**47.30%**
Agonum muelleri	0.030036	-0.33395	0.418154
Bembidion atrocaeruleum✓	0.502376	0.189831	-0.17119
B.decorum✓	0.376347	-0.0121	-0.07917
B.monticola✓	0.360592	0.403301	-0.12208
B.prasinum✓	0.003631	0.215831	0.587354
B.punctulatum✓	0.187543	-0.0003	0.593352
B.tetracolum	0.36714	-0.25085	0.158478
B.tibiale✓	0.411238	0.175185	0.037873
Nebria brevicollis	0.076554	-0.39095	-0.21456
Paranchus albipes	0.351118	-0.38722	-0.05694
Larva✓	0.082546	-0.49665	-0.04232

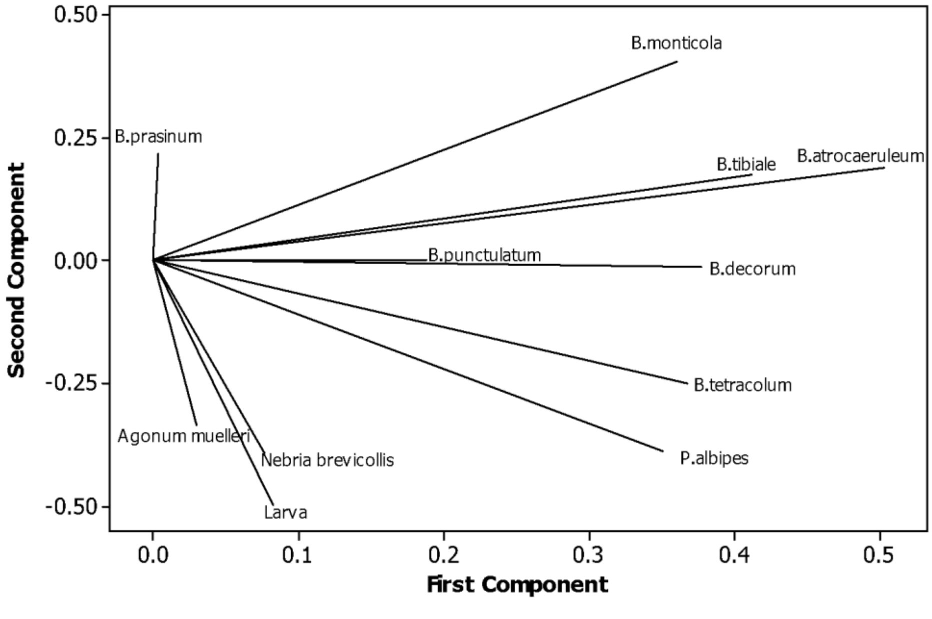


Figure 4.4 Species distribution on the first two principal components of beetle abundances over three years at six sites in the Usk river system, Wales (see *Table 4.3* for loading values).

Table 4.4 Loading values of dominant habitat variables (shaded) onto three principal components (correlation matrix) describing habitat character at six ERS sites in the Usk river system over three years.

	HabPC1	**HabPC2**	**HabPC3**
Eigenvalues	**3.81**	**2.62**	**2.00**
Cumulative proportion	**27.20%**	**45.90%**	**60.20%**
Bare	0.052724	-0.47432	-0.39449
Ground Cover	-0.13158	0.433683	0.416832
Scrub	0.221948	0.138929	-0.00296
Canopy	0.157736	0.068475	-0.13141
Flat	0.355582	-0.1847	0.297586
Gentle	-0.39155	0.159116	-0.16899
Steep	0.055274	0.061033	-0.46405
Simple	-0.09684	-0.4677	0.290742
Humped	0.058947	0.467122	-0.27544
Complex	0.109715	0.211233	-0.08855
Shore length	0.380084	0.051153	-0.13799
Width	0.271463	0.101504	0.297119
Area	0.442246	0.069864	0.118705
Heterogeneity	0.42934	-0.02064	-0.17679

4.3.4 Variations in Habitat Conditions through Time

General linear modelling confirmed large spatio-temporal variation in habitat character between sites ($F_{5,\,131}$ = 1479.82, $p < 0.001$) and years ($F_{2,\,131}$ = 12.58, $p < 0.001$, R^2 adj' = 98.26%; *Figure 4.6*) during years of progressively low river discharge. Ground cover increased during the study period (*Figure 4.6a*) as shore length increased and ERS area fluctuated (*Figure 4.6e, g*); whilst flatter and humped topography declined (*Figure 4.6b, d*).

Beetle assemblages and habitat character

Although beetle assemblages were linked to some aspects of habitat character, variations between years were far stronger no matter what habitat measures were used as covariates (*Table 4.5*). Species richness varied particularly strongly among the study years, increasing between 2009 and 2011 (e.g., with conditions provided under habitat PC 1, $F_{12,\,131}$ = 4.84, $p < 0.001$, R^2 adj' = 29.49%). Among individual species, *B. decorum* and *B. punctulatum* increased in abundance over the study period, though this was only statistically significant for the former, irrespective of habitat co-variables (e.g., with conditions provided under habitat PC 1, $F_{12,\,131}$ = 2.79, $p < 0.01$, R^2 adj' = 28.24%; *Figure 4.3* and *Table 4.5*). *Bembidion punctulatum* abundance varied significantly between sites (e.g., with conditions provided under habitat PCs 2 and 3, $F_{5,\,131}$ = 5.59, $p < 0.001$, R^2 adj' = 20.57%). By contrast, both inter-annual and inter-site increases in *B. prasinum* abundance appeared to associate with conditions provided under habitats PCs 1 and 3, exposed by declining river discharge ($F_{5,\,131}$ = 5.44, $p < 0.001$, R^2 adj' = 20.65%, and $F_{12,\,131}$ = 1.98, $p < 0.05$, R^2 adj' = 21.7% respectively). Of the four principal species, *Bembidion atrocaeruleum* abundance showed weakest associations to inter-annual dynamics in habitat PC3. Inter-annual assemblage abundance was associated with variations in habitat PC1 ($F_{12,\,131}$ = 7.74, $p < 0.001$, R^2 adj' = 42.01%). Of the species principal components, the first and second components were associated with inter-annual and inter-site variation (e.g., for species PC1, $F_{12,\,131}$ = 9.31, $p < 0.001$, R^2 adj' = 45.56%), whilst the third species component, dominated by *B. prasinum* and *B. punctulatum*, associated only with inter-site variation ($F_{5,\,131}$ = 6.04, $p < 0.001$, R^2 adj' = 24.02%), reflecting variations in the extent of exposed sediment adjacent to the shoreline.

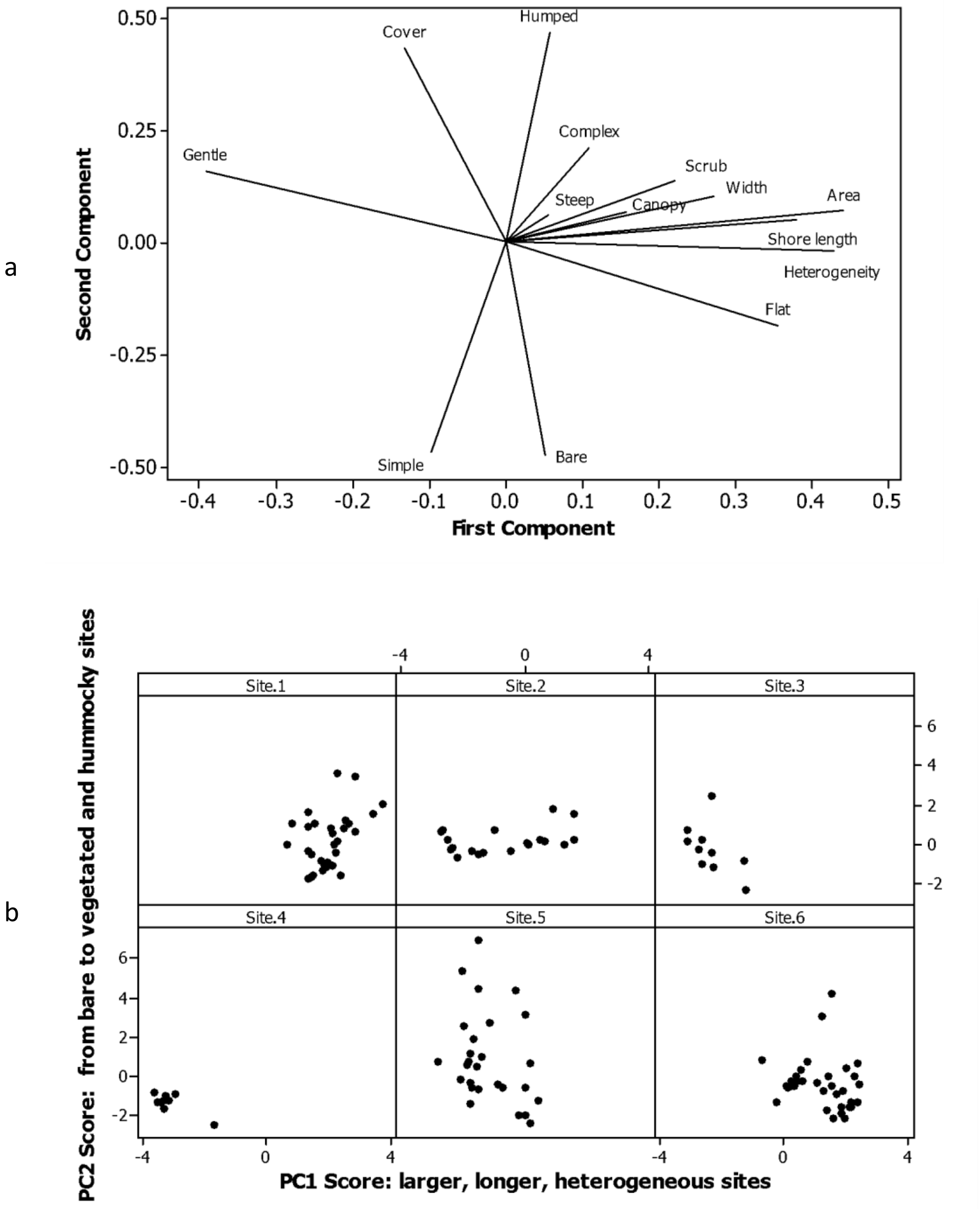


Figure 4.5 a) The PCA biplot of habitat variables on two principal components over a three year study in the Usk river system (see *Table 4.4* for habitat loading values). b) Correlation between samples and habitat distribution on each site; Sites 1 and 6 were most coincident with the co-linear habitat variables.

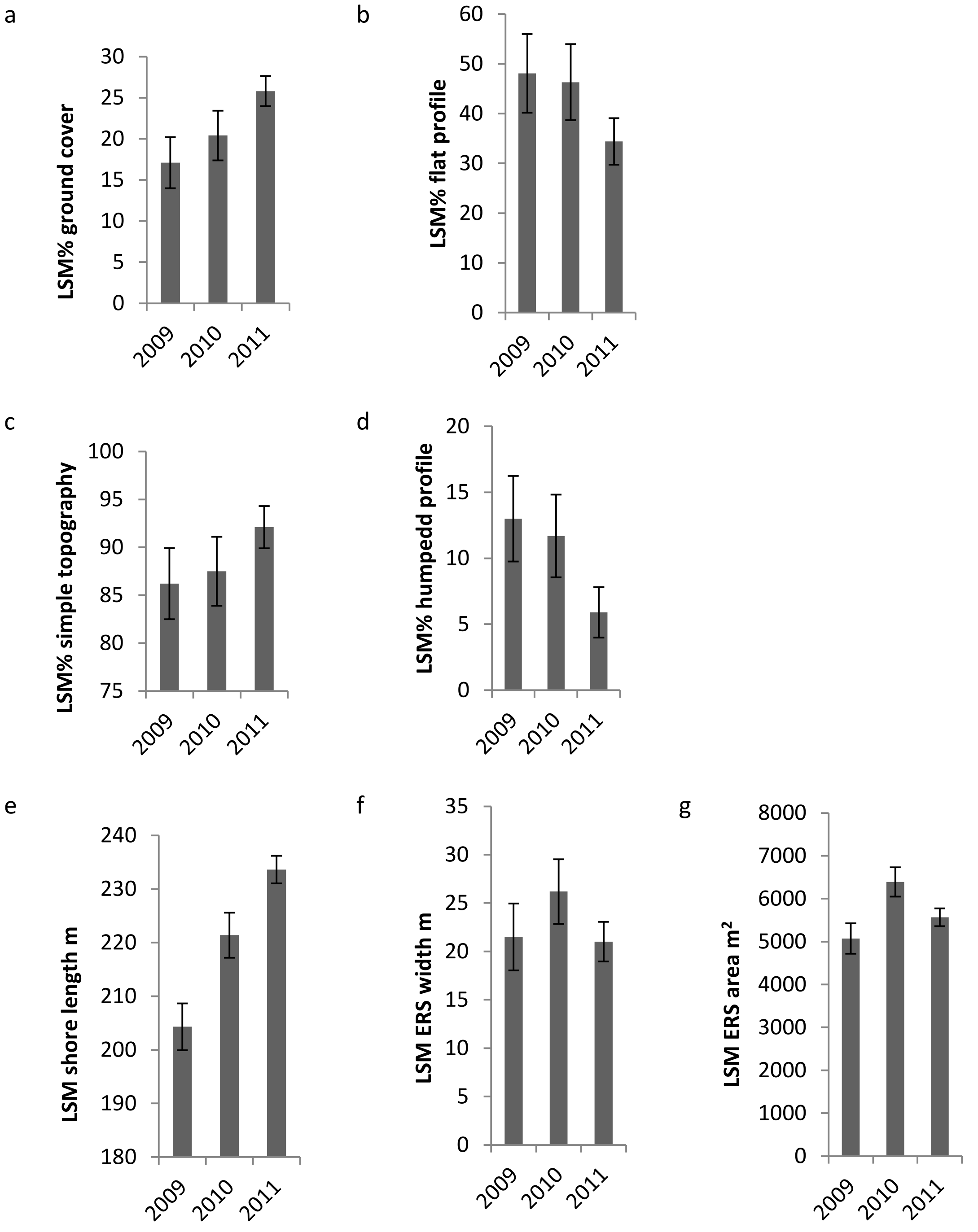


Figure 4.6 Annual distribution of the dominant habitat variables (as least squares means LSM) within principal components (*Table 4.4*). a) ground cover; b) flat ERS profile; c) simple ERS topography; d) humped ERS topography; e) ERS shore length m; f) ERS width m; g) ERS area m^2

Table 4.5 Species responses to variations among years, between sites and within-sites during three years, based upon general linear models (log(n + 2) transformation) and Akaike's Information Criterion (AIC). AIC values ranked for a) species richness, b) abundance, c) four principal species and d) species principal components. Significance levels indicate * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. See data displays in *Figuress 4.3 – 4.6*.

GLM ranked by AIC values

	Species Factor	**Model (* significance) and direction of change ↑ ↓**	**Habitat covariate (* significance)**	**AIC value**
a	Spp richness	Year(Site)*** ↑	HabPC1*	-482.80
	Spp richness	Year(Site)*** ↑	HabPC2	-481.26
	Spp richness	Year(Site)*** ↑	HabPC3	-479.49
b	Abundance	Year(Site)*** ↓	HabPC1*	-34.05
	Abundance	Year(Site)***	HabPC2	-26.10
	Abundance	Year(Site)***	HabPC3	29.46
c	*B. decorum*	Site*** ↓ downstream, Year(Site)** ↑	HabPC1	-367.65
	B. decorum	Site*** Year(Site)***	HabPC3	-367.65
	B. decorum	Site*** Year(Site)***	HabPC2	-367.61
		Site*** varied between sites	HabPC3	-324.88
	B. punctulatum			
	B. punctulatum	Site***	HabPC2	-323.08
	B. punctulatum	Site**	HabPC1	-322.92
		Year(Site)* ↑	HabPC3***	-293.62
	B. prasinum			
	B. prasinum	Site*** ↓ downstream, Year(Site)*	HabPC1***	-291.87
	B. prasinum	Site*	HabPC2	-275.73
		Year(Site)*** ↓	HabPC3*	-232.75
	B. atrocaeruleum			
	B. atrocaeruleum	Year(Site)***	HabPC1	-229.75
	B. atrocaeruleum	Site** varied between sites, Year(Site)***	HabPC2	-227.76
d	SpPC3	Site*** varied between sites	HabPC1*	-5.29
	SpPC3	Site**	HabPC3	-4.37
	SpPC3	Site***	HabPC2	-2.10
	SpPC2	Site*varied between sites, Year(Site)*** ↓↑	HabPC3**	1.18
	SpPC2	Year(Site)***	HabPC2*	6.18
	SpPC2	Year(Site)***	HabPC1	8.63
	SpPC1	Site* varied between sites, Year(Site)*** ↓		
	SpPC1	Year(Site)***	HabPC1	15.06
	SpPC1	Year(Site)***	HabPC2	15.17

4.4 Discussion

This study examined how carabid assemblages responsed to localised environmental change, during a period of prolonged river discharge stability, when there was an absence of fluctuations between aquatic and terrestrial conditions necessary to maintain ERS (Henshall *et al.* 2011). Whilst this study did not directly test the role of discharge variation, during this three year period, habitat conditions changed significantly, with an increase in shore length, exposed river bed and encroaching ground cover being of particular note. The study tested the hypothesis that local habitat character had larger effects on carabid assemblages than river discharge variations within and between years. Results showed that temporal and spatial availability of ERS, affected by inter-annual variations in river discharge, had larger effects than local habitat character. Ground cover, ERS width and flat profile increased in two principal components, suggesting a dynamic relationship between river discharge and ERS terrestrialisation (i.e., wide and flat sediment availability extended behind retreating river discharge, providing space for ground cover to encroach further).

Of all carabid responses, species richness varied most strongly each year, in response to survey year and variations between sites. However, with analysis based upon those species occurring in > 5% of samples, and approximately 80% of annual assemblages dominated by just four species, further analysis is required for evidence of species succession in the absence of regular inundations events (Bornette and Amoros 1996; Gergely *et al.* 2001; Bates *et al.* 2006); this is examined further in Chapter 5. Of four abundant ERS specialists, *B. decorum* abundance varied the most between sites and years, showing no significant response to habitat variation. *Bembidion punctulatum* varied between sites but not years and was also non-responsive to habitat variation. *Bembidion prasinum*, varying between sites and years, responded very strongly to habitat variability, in particular to the availability of flat, simple and wide ERS as river discharge retreated and ground cover advanced. This suggested a particular response to the availability of early succession conditions on freshly exposed river bed, and a possible role as an indicator species for fresh, primary ERS habitat. The most abundant and ubiquitous species, *B.*

atrocaeruleum, a ‘generalist specialist’ of ERS (Bates *et al.* 2006), declined in abundance each year as the other three species increased; suggesting a general decline in ERS suitability but an increase in extent of particular conditions favoured by *B. prasinum* and *B. punctulatum* in the third principal component (i.e., early succession conditions on freshly exposed sediments revealed by retreating river discharge). *Bembidion atrocaeruleum* is known to exert a competitive advantage and a rapid within-year spatial response to change facilitated by its abundance (Bates *et al.* 2006). It is known to fly readily and was observed to do so regularly during surveys (*pers. obs'*). The weaker GLM model for this species reflected its ubiquitous and abundant distribution. Abundance variations for these species might also reflect varying life histories. Evidence on life histories, however, is lacking in the literature.

Low levels of beta-diversity suggested by the modest results from initial unimodal analyses (NMDS and DCA), in combination with the strong linear effects of time and space highlighted by PCA, suggested meta-assemblage dynamics affecting specialist Carabidae in this study area. Species responses to transient patches of optimal environmental variables are likely to be unimodal, but at a larger spatio-temporal scale than the reach used in this study. During this study, rather than surveying across an environmental gradient, for example working perpendicularly up shore away from the water’s edge (Bates *et al.* 2007b), surveys were targeted deliberately within the optimal activity zone adjacent to the water, where sediment wetness and water proximity increased the likelihood of encountering aquatic food subsidies and leaf litter (Ruggiero *et al.* 2009; Henshall *et al.* 2011), and where ERS specialists congregate accordingly. Under these conditions, a linear rather than unimodal response for faunal abundance might be predicted. This study argues that a larger area, for example catchment rather than reach, is required to identify unimodal spatial responses and differentiate beta- from alpha diversity on ERS in the River Usk. The optimal duration of ideal environmental conditions for ERS specialists would also be revealed by a longer study period. Nonetheless, it is possible that during this study species may have synchronised responses to time and space and this is examined in Chapter 5.

In accordance with other studies (Sadler and Bell 2000; Sadler *et al.* 2006), habitat variables for this study were recorded on a percentage cover/estimated dimension basis, plus a heterogeneity category, to provide a comparative assessment by proportion between sites and years, of the changing habitat dynamics available to ERS specialists. Despite there being very significant inter-annual and inter-site habitat variability, variation recorded this way proved in general to be too modest to register a significant influence on species. This suggests that fauna are responding spatio-temporally to other signals influenced by annual/seasonal and spatial scale changes, for example weather, relative humidity, surface wetness (sediment moisture), and food subsidy. Some of these are examined further in Chapter 6.

Faunal responses to inter-site and inter-annual variation indicated that conservation management is required at a catchment scale, over a prolonged time frame. Whilst the distribution and extent of ERS and diversity and abundance of arthropods are declining (Paetzold *et al.* 2008; O'Callaghan *et al.* 2013b), localised within-site conservation management is unlikely to retain the range and scale of environmental variables required for favourable conservation status of ERS and their specialist fauna. Studies are required of entire river corridors, and nested reaches within them to determine the appropriate scale for management intervention (Larsen *et al.* 2009; Clews *et al.* 2010); to examine the relationship between meta-assemblage composition and the terrestrial-aquatic phases in the riparian ecotone; to identify a suite of “conservation status” indicator species, such as *B. prasinum* and *B. decorum*; and to attribute ecological and geomorphological variation to events in the wider floodplain (Larsen 2010). The status and extent of exposed riverine sediments within a river catchment provide a convenient series of ‘rapid assessment ecological sentinels’ to record the rate of ‘riparian squeeze’ and a river’s recovery from this following management intervention at a catchment scale.

Findings in this study contrasted with findings on other rivers within the same river basin, where habitat variables such as substrate type, percentage cover of fine sediments, median sediment size, habitat heterogeneity and frequency of livestock trampling influenced species distribution and abundance (Sadler *et al.* 2004); with a range of micro-habitats found to be influenced by surface temperature and humidity, inundation frequency, availability of aquatic food subsidies, variation in ground cover and sediment size (Bates *et al.* 2007b). Two of these micro-habitat variables are investigated in Chapter 6.

Whilst the habitat variables used in this study appeared to have only a marginal effect on assemblage distribution patterns, life history traits of ERS specialists do interact at different spatial scales with environmental variables (Gerisch 2011; Gerisch *et al.* 2012). For example, whilst the influence of laterally graded environmental variables (humidity, inundation frequency, surface temperature, and availability of aquatic food subsidies) has been well described (Desender 1989; Paetzold *et al.* 2005; Bates *et al.* 2007b), the influences of sediment size, vegetation cover, elevation, shade and livestock trampling, whilst having been investigated (Bates and Sadler 2005; Bates *et al.* 2005; Bates *et al.* 2006; Sadler *et al.* 2006; Bates *et al.* 2007a; 2007b; Lambeets *et al.* 2008a; 2008b; Bates *et al.* 2009; Henshall *et al.* 2011; Baiocchi *et al.* 2012) merit further study, in particular over the sort of large scale involving several ERS sites that the space and time results in this study suggest.

5 Ecological Succession in Terrestrial Carabid Beetles on Exposed Riverine Sediments (ERS)

Summary

Riparian ecosystems are naturally dynamic but also sensitive to the effects of river modification and abstraction. These effects are particularly marked in exposed riverine sediments (ERS): point, lateral or mid-channel bars of graded fluvial sediments, whose formation requires regular hydrological events that can be impeded by flow modification. Whilst there have been studies of ecological succession among carabid beetles along environmental gradients, few have considered the effects of flow stabilisation on the characteristic invertebrate assemblages of ERS and any potential implications for conservation. This study examined successional change in specialist ERS Carabidae over a three-year period of stable flow in the Usk system, Wales (UK). During three sample visits in each of three years (2009-11), carabid beetles were sampled from six ERS sites at 27 sample locations spaced at 50 m intervals along the shoreline. General linear models were used to investigate evidence for inter-annual assemblage succession among specialist and generalist species. Mean Individual Biomass (MIB), which measures changing body size within assemblages and has been previously assumed to show progression towards stable conditions, was also included in the GLM to identify succession. Results revealed a progressive annual decline in species richness of specialist carabids of ERS over the study, accompanied by a sharp increase and then slight decline in the abundance and species richness for generalist species. Mean Individual Biomass tracked the annual abundance of generalist species. A clear annual pattern of increasing MIB, accompanied by declining species richness and abundance of ERS specialists was not observed, and the dominant specialists remained resilient within the assemblage each year. In conclusion, this study was unable to detect clear evidence for faunal succession tracking possible habitat succession on ERS during a three year period of river discharge stability. Whilst it is possible that MIB might prove a useful means of detecting such change, a longer study period than three years is required to achieve this. Nevertheless, in the knowledge that other studies have relied on changing average carabid body size to track environmental gradients, the method of tracking increasing MIB on ERS, to detect environmental stabilisation within riparian ecosystems, merits further study.

Key words: Beetles, *Bembidion*, Discharge, Mean Individual Biomass, Regulation, Riparian, River Usk, Succession.

5.1 Introduction

As a consequence of fluctuating water levels, exposure, submersion, erosion, and flows of energy and matter, rivers and their riparian ecosystems are in a perpetually dynamic state (Rabeni and Sowa 2002). This is particularly true of exposed riverine sediments (ERS), which are typically highly disturbed, re-sorted and re-distributed by regular flood events and bed movement during high discharge (Bates and Sadler 2005; Bates *et al.* 2005; Bates *et al.* 2006; O'Callaghan *et al.* 2013b). Consequently, faunal abundances on ERS do not reach levels at which inter-specific competition occurs (Bates *et al.* 2005), and discharge fluctuations and associated events are expected to maintain a dynamic steady state (Thorp *et al.* 2006). These circumstances can be considered highly conducive to ecological succession, with populations and assemblages fluctuating between relative disturbance and stability (Rabeni and Sowa 2002). Indeed, the natural flow dynamics that determine when and where ERS occurs mean that disturbance and ecological succession are natural, expected features of their characteristic assemblages.

By contrast, human modifications to river catchment ecosystems risk causing both decreasing stability, for example through catchment drainage, or, alternatively, increasing it, for example through abstraction (Paetzold *et al.* 2008; O'Callaghan *et al.* 2013b; Guareschi *et al.* 2014). Such changes have particularly marked effects on riparian ecosystems (Paetzold *et al.* 2008) and their specialised riparian organisms (Bates *et al.* 2009; Henshall *et al.* 2011). Altering the dynamic steady state of riparian systems, for example in regulated rivers, is expected to change both habitat succession and faunal assemblage structure (Compton 2002; Rolls *et al.* 2012). Allogenic and deterministic factors such as flow regulation, global warming (Bates *et al.* 2009) and channel modification (Paetzold *et al.* 2008), might all have a negative influence on the regularity of flood events, and therefore on the abundance and composition of representative species (Paetzold *et al.* 2008; McCluney and Sabo 2012). Persistent low flows, which expose new areas of sediment and prevent disturbance, are expected also to be followed by the additional stabilising influence of terrestrial vegetation growth (Gergely *et al.* 2001; Bates *et al.* 2006). Such vegetation is likely to modify further the extent and condition (e.g., wetness) of available habitat for representative fauna such as specialist Carabidae (Fowles 2004). Where persistent low flows are repeated annually, this might be sufficient to remove the pulses of regular disturbance vital to the ecological viability of ERS and their specialist fauna, with consequences for distribution patterns and exchanges of energy and materials (Bates *et al.* 2006; Rolls *et al.* 2012). So far, however, whilst there have been studies of succession within carabid assemblages along environmental gradients (Gray 1989; Braun *et al.* 2004; Ulrich *et al.* 2008), the possible successional effects of flow stability on ERS organisms are poorly described and understood.

Taking advantage of a three-year period of stable flow in the Usk river system (Wales, UK), this chapter examined the hypothesis that successive periods of low river discharge will be accompanied by ecological succession within ERS carabid assemblages. Given that the dynamics of ERS should interrupt faunal succession where it occurs (Bates *et al.* 2006), any evidence that it persisted would indicate increasing stability, and reduced suitability for ERS specialists.

As well as structural changes within assemblage composition, evidence for succession was sought from patterns in Mean Individual Biomass (MIB). In previous studies, significant changes to MIB values in a time series have been used to indicate faunal ecological succession (Cardenas and Hidalgo 2007; Jelaska *et al.* 2011), whilst by inference, absence of this effect indicates ecological resilience. For example, MIB measured on carabid beetles has been used to observe the ecological age of neighbouring woodland habitats along a succession gradient controlled by different management regimes (Schwerk and Szyszko 2007, 2009). In this study, therefore, evidence for faunal succession within assemblages would be demonstrated by a combination of increasing MIB, declining abundance and species richness of ERS specialists and increasing abundance and species richness of generalist species.

5.2 Methods

5.2.1 The Study Area and Beetle Sampling

The general physical and hydro-geomorphological characteristics of ERS, and specific aspects of the six sites that made up the study area, have been described already (Chapter 4). Briefly, the River Usk lies within a catchment modified by impoundment and considerable water abstraction (EAW 2007) that are likely to affect habitat character and faunal succession on ERS.

Using the timed hand searching procedure described in Chapter 4, carabid beetles were sampled from sample locations at each of six sites three times per year for three years, between 2009 and 2011, and identified to species level. Samples were taken exclusively adjacent to the water's edge, with sample locations spaced at 50 m intervals. This provided a dataset totalling 4393 beetles of 27 distinct species and 11 ERS specialists (Fowles 2004); larvae were also sampled but grouped as a quasi-species "larvae" and treated as an ERS specialist species. Species identified as ERS specialists versus generalist species are listed in *Appendix 4*.

5.2.2 Determining Mean Individual Biomass

Ideally, ecological succession among ERS Carabidae would be assessed through an in-depth understanding of the ecology and life history traits of individual species. Whilst some literature exists on single species or narrow groups of carabids (e.g., Andersen 1968, 1970, 1978, 1983a, b, 1985, b, 1986, 1988, 1989; Manderbach and Hering 2001; Bates and Sadler 2005; Bates *et al.* 2005; Van Looy *et al.* 2005; Andersen 2006; Sadler *et al.* 2006; Bates *et al.* 2007b; Kleinwaechter and Rickfelder 2007; Van Looy *et al.* 2007; Kleinwachter and Burkel 2008; Ramel 2008; Andersen 2011b; Andersen 2011a; Gerisch 2011; Fowles 2004), this is not comprehensive and carabid life history is poorly understood (Luff 2005, 2007). Consequently, whilst investigating changing species composition offers some understanding of succession within assemblages (see data analysis below), this cannot yet be backed up with life history evidence.

Mean individual body size of carabids is known to decline along gradients of increasing environmental disturbance (Gray 1989; Braun *et al.* 2004; Ulrich *et al.* 2008); so conversely, it will increase with increasing environmental stability. On this basis, Mean Individual Biomass (MIB) (Schwerk *et al.* 2006) assesses differences among assemblages in habitats of different successional age (Cardenas and Hidalgo 2007; Schwerk and Szyszko 2007; Jelaska *et al.* 2011; Kwiatkowski 2011), quality or natural state (Schwerk *et al.* 2006). Higher MIB values are taken to indicate more mature habitats or later succession stage. On ERS this can be assumed to indicate that smaller, specialist Carabidae of ERS are being replaced by larger, generalist species, inflating MIB values. For a species assemblage, MIB is defined as *total biomass of all individuals in a sample ÷ total number of individuals in the sample* (Schwerk and Szyszko 2007). With the dataset for this study accumulated from six sites during three years, variations in MIB could be examined on subsets of this (subsets listed below). Body weight for each species was calculated using the equation:

$$\ln y = -8.92804283 + 2.55549621 \times \ln x$$

where y is an individual beetle's live estimated body weight (mg) and x the body length of that individual (Schwerk and Szysko 2007). Body length for each beetle species was estimated using the mid-length within the range given by Luff (2007). For example, *Bembidion atrocaeruleum* body length is given as 4.5 – 5.5mm, therefore the estimated mid-length was 5.0mm. Thus, for this species, live estimated body weight was:

$$\ln y = -8.92804283 + 2.55549621 \times \ln 5.00 \text{ mm}$$

y = 8.1 mg = live body weight *B. atrocaeruleum.*

Mean Individual Biomass was then calculated by summing the biomass for each subset and dividing by the total number of individuals in that subset. Data subsets investigated from the full dataset were based on species richness and total abundance from each site of:

All species sampled each year

All ERS specialists sampled each year

Generalist species sampled each year

All species present in > 5% of sample locations each year

ERS specialists present in > 5% of sample locations each year

Generalist species present in > 5% of sample locations each year.

All species apart from ERS specialists (Fowles 2004) were treated as generalists.

5.2.3 Data Analysis

Species richness, abundance and MIB in each of the above data subsets, treated as dependent variables, were investigated by general linear modelling (GLM), using year and site as independent factors. Directions of change were identified using least squared means. All data were normalised by log (n + 2).

All statistical analyses were completed using Minitab 16®.

5.3 Results

General linear modelling demonstrated that whilst there was no significant gradient among years in species richness within the entire species dataset, variation among years was evident in species richness for generalist species present in over 5% of samples and in all samples ($F_{2,\ 236} = 3.62$, $p < 0.05$ and $F_{2,236} = 4.16$, $p < 0.05$), with a sharp increase between 2009 and 2010. This was accompanied by a declining annual gradient in species richness for ERS specialists present in >5% of samples and in all samples ($F_{2,\ 236} = 3.04$, $p < 0.05$ and $F_{2,\ 236} = 2.85$, $p = 0.06$; *Tables 5.1* and *5.2*, and *Figure 5.1*). This inter-annual pattern was evident for the MIB variations among generalist species in over 5% of samples and in all samples ($F_{2,\ 17} = 3.52$, $p = 0.07$ and $F_{2,\ 17} = 5.59$, $p < 0.05$) but not among ERS specialists.

Variation among years was also evident for abundance of generalist species in over 5% of samples and in all samples ($F_{2,\ 236} = 5.62$, $p < 0.01$ and $F_{2,\ 236} = 5.14$, $p < 0.01$, respectively), with the same sharp increase between 2009 and 2010 (*Figure 5.1*). Inter-annual variations in abundance were stronger than for species richness or MIB (*Table 5.1*). In contrast to the inter-annual decline in species richness for ERS specialists, there were no significant gradients for inter-annual abundance of ERS specialists.

Whilst there were no obvious gradients between sites, inter-site variation was most evident in the abundance of all species present in over 5% of samples ($F_{5,\ 236} = 3.75$, $p < 0.01$), followed by the MIB of ERS specialists and generalists ($F_{5,\ 17} = 3.56$, $p < 0.05$ and $F_{5,\ 17} = 2.85$, $p = 0.075$, respectively), and then the species richness of ERS specialists ($F_{5,\ 236} = 2.54$, $p < 0.05$).

Whilst inter-annual and inter-site variations were evident in MIB of subsets, there were no inter-annual gradients in annual MIB (*Figure 5.1*). There was a sharp increase in the MIB for all species, all generalist species and generalists present in over 5% of samples between 2009 and 2010 ($F_{2,\ 17} = 6.16$, $p < 0.05$, $F_{2,\ 17} = 5.59$, $p < 0.05$ and $F_{2,\ 17} = 3.52$, $p = 0.07$, respectively), which tracked the annual variations in abundance of generalists.

Table 5.1 GLM showing variations in carabid species richness, abundance and Mean Individual Biomass (MIB) following three years of sample visits across six sites visited three times per year. Significance levels indicate * $p < 0.05$ and ** $p < 0.01$.

Data subset		Spp richness	Abundance	MIB
All species	Year	NS	NS	*
	Site	NS	NS	NS
All ERS specialists	Year	p = 0.06	NS	NS
	Site	*	NS	*
All generalist species	Year	*	**	*
	Site	NS	NS	p = 0.075
Spp in >5% samples	Year	NS	NS	NS
	Site	NS	**	NS
ERS specialists in >5% samples	Year	*	NS	NS
	Site	*	NS	NS
Generalist species in >5% samples	Year	*	**	p = 0.07
	Site	NS	NS	NS

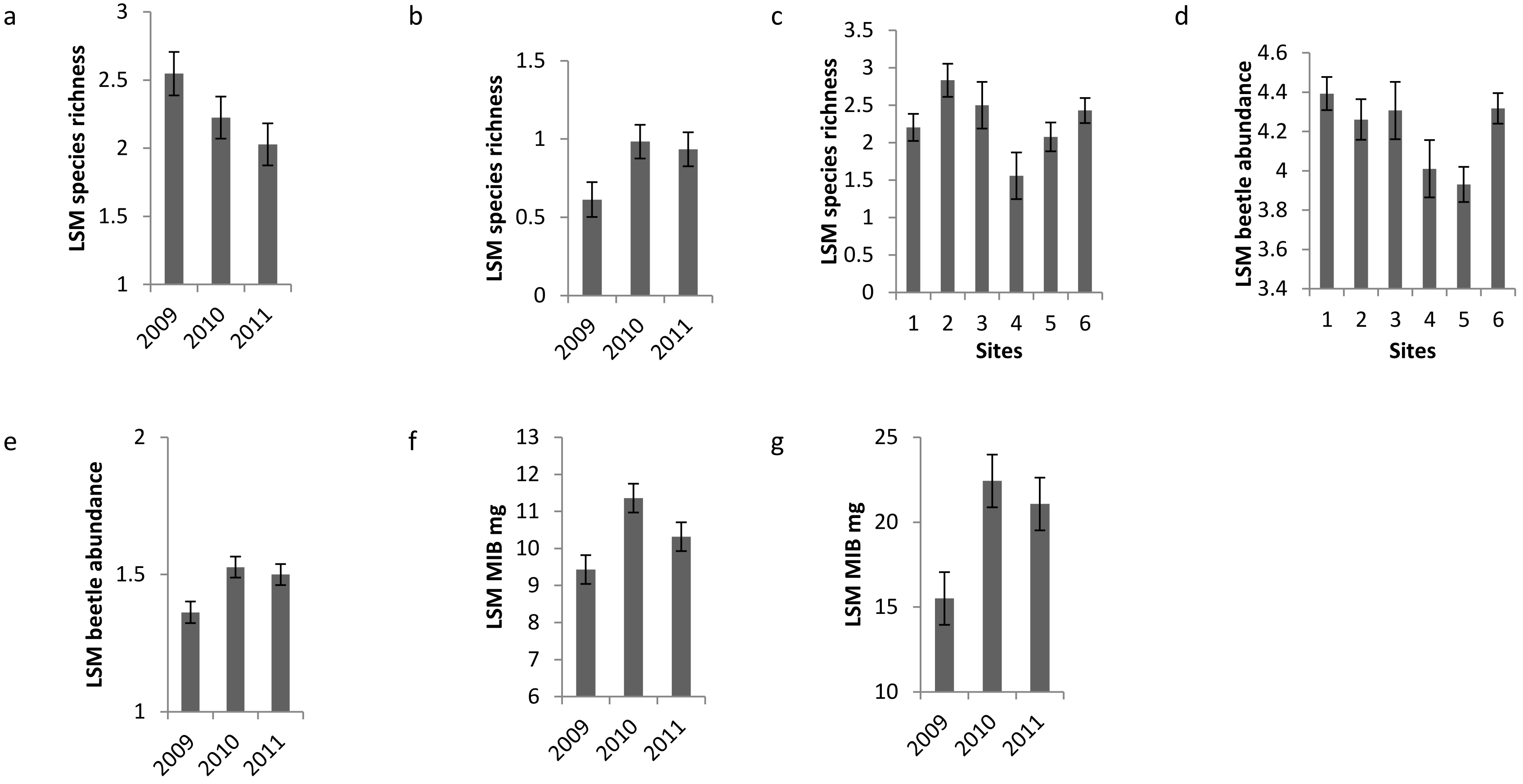

a
LSM species richness
3
2.5
2
1.5
1
2009
2010
2011
b
LSM species richness
1.5
1
0.5
0
2009
2010
2011
c
LSM species richness
3.5
3
2.5
2
1.5
1
0.5
0
1
2
3
4
5
6
Sites
d
LSM beetle abundance
4.6
4.4
4.2
4
3.8
3.6
3.4
1
2
3
4
5
6
Sites
e
LSM beetle abundance
2
1.5
1
2009
2010
2011
f
LSM MIB mg
13
12
11
10
9
8
7
6
2009
2010
2011
g
LSM MIB mg
25
20
15
10
2009
2010
2011

Figure 5.1

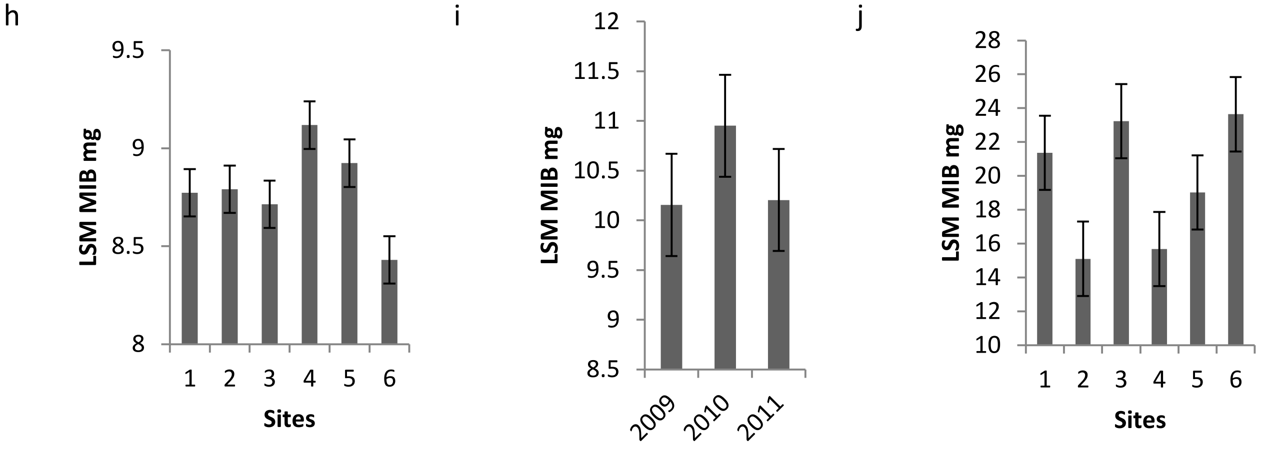


Figure 5.1 Inter-annual and inter-site gradients in species richness, beetle abundance and Mean Individual Biomass (MIB, mg live weight) illustrated by least squares means (LSM) and standard error. Where gradients for all species and for those present in > 5% of samples were equivalent, only those for species in > 5% of samples are illustrated (see also *Tables 5.1* and *5.2* for GLM and AIC values). a) ERS specialist species richness > 5% of samples; b) generalist species richness > 5% of samples; c) ERS specialist species richness > 5% of samples (inter-site variation); d) abundance all species > 5% of samples (inter-site variation); e) generalist abundance > 5% of samples; f) MIB all species; g) MIB generalist species; h) MIB ERS specialists (inter-site variation); i) MIB generalist species > 5% of samples; j) MIB generalist species (inter-site variation).

5.4 Discussion

Chapter 4 established that stable river discharge, and inter-annual and inter-site variation, influenced carabid assemblage distribution more than intra-site variation. This chapter examined the hypothesis that successive periods of low river discharge would be accompanied by ecological succession within ERS carabid assemblages, requiring persistent inter-annual succession indicative of increasing environmental stability and declining ERS suitability for specialist carabids. By investigating inter-annual and inter-site variations in species richness, beetle abundance and Mean Individual Biomass in entire and sub-categorised datasets, no clear evidence was established of succession within carabid assemblage structure. There was a sharp increase in species richness and abundance of generalist species between the first and second survey years, and a slight decline in year three, tracked by MIB. This did not, however, demonstrate an annual trend towards larger generalist species tracking increasing terrestrialisation of, and encroaching ground cover on, ERS during repeated stable periods of low river discharge.

This study investigated fluctuations between disturbance and stability and how this affects ecological succession but results proved inconclusive. Having established in Chapter 4 that the three year study coincided with a period of relative discharge stability, the expectation was that succession would proceed apace. Whilst Chapter 4 found putative evidence of increasing terrestrialisation (ground cover encroachment), the effects of this were masked by larger inter-annual and inter-site effects on species distribution. This led to the supposition for this chapter that the inter-annual effect might be reflected by inter-annual faunal succession, which was not supported conclusively by the results.

There was however, a putative relationship between annually declining species richness for ERS specialists accompanied by increasing richness and abundance of generalist species. Mean Individual Biomass tracked the patterns for generalist rather than specialist species, where MIB increased as the abundance and frequency of larger generalist species increased. Clear evidence of succession required patterns showing successive annual declines in ERS specialist richness and abundance, accompanied by annual increases in MIB as generalist species supplanted specialists. These patterns were not observed. Instead, there was resilience in the ERS specialists present in over 5% of samples, reflecting the numeric resilience of four principal species (Chapter 4), with succession pressure likely to be exerted on rarities and singletons.

In the knowledge that carabid beetle distribution, abundance and adaptable life history traits make them suitable indicators of habitat quality and environmental change, their average body size has been used to investigate changing environmental gradients, for example recording smaller individuals on polluted sites and larger individuals on stabilised sites (Braun *et al.* 2004). Several studies have recorded a similar pattern on environmental gradients from rural environments supporting larger individuals, to urban or human-disturbed environments supporting smaller, readily dispersing individuals (Gray 1989; Alaruikka *et al.* 2002; Ulrich *et al.* 2008); specialists of ERS also disperse readily during disturbance (Bates *et al.* 2006). Despite lacking clear evidence of faunal succession through larger average body size during three years, it is possible to surmise that increasing average carabid body size on ERS is indicative of declining environmental stress because naturally disturbed habitats should favour smaller r-strategists (Kotze *et al.* 2003). Increasing carabid body size on ERS through time might therefore be an early detection of ERS ecosystem decline, with an added indication of habitat succession and stabilisation shown by the increasing proportion of generalist species (Buchholz *et al.* 2013). The departure in this study was that smaller MIB would have indicated preferable conditions for ERS specialists, which are reliant on regular disturbance and re-sorting of sediments to maintain early succession conditions (Bates and Sadler 2005).

Given the importance of ERS as conjunction zones for riparian biodiversity (Henshall *et al.* 2011), declining ERS suitability for specialist fauna would indicate a decline in overall riparian biodiversity and the potential vulnerability of the River Usk to the effects of prolonged low flows anticipated as a consequence of human-induced climate change (Capon *et al.* 2013). The principal environmental variable maintaining the typical early succession steady state on ERS is high river discharge producing regular inundation events (Sadler *et al.* 2006). Riparian Carabidae will occur throughout the river system provided regular flood events continue (Bonn *et al.* 2002; Lambeets *et al.* 2008b; 2009); with flood duration and groundwater depth influencing species assemblage structure and distribution (Gerisch *et al.* 2006). Amongst ERS specialists, more mobile species such as *B. atrocaeruleum* dominate the preferred open and temporary assemblages whilst suitable habitat dynamics persist locally (Hengeveld and Hemerik 2002). Whilst not conclusive, results from this study and from Chapter 4 suggest that as habitat succession driving assemblage succession continues, ERS specialists remain resilient within a narrower spectrum of ERS suitability. The most abundant species declined each year whilst three other principal species increased in numbers, albeit at much lower abundance levels, reflecting a narrower suitability spectrum (*Figure 4.3a*). It is possible that these species would become functionally isolated as the encounter rate between species and habitat declines with declining ERS suitability. Further annual and seasonal field work would elucidate the point at which ERS suitability across a suite of sites reaches a critical threshold below which ERS specialists become functionally extinct.

Inter-annual and inter-site variability have been demonstrated to exert a stronger influence on carabid assemblage distribution patterns than within-site variability (Chapter 4) but evidence did not clearly emerge for assemblage succession in response to inter-annual and inter-site variability. On ERS, a longer study period than three years is required to investigate gradients in species richness, faunal abundance and MIB that are indicative of faunal succession within early stage habitats such as ERS. The results in this study suggest that MIB might yet be a valid method for comparing the 'ecological age' of ERS but that a longer study period is required to establish its usefulness. By contrast with other short term studies between neighbouring, managed environmental gradients (Jelaska *et al.* 2011), and in the absence of autoecological evidence about the relative position of different ERS specialists along the succession continuum, MIB did not yet prove to be an effective substitute for species life history traits.

6 An Experimental Evaluation of Local Subsidy Effects on Riparian Carabidae (Coleoptera)

Summary

River ecosystem function is affected by nutrient flux, flow regulation, climate change and habitat modification, all of which can influence faunal assemblages. The riparian zone is particularly sensitive, for example where exposed riverine sediments (ERS) support assemblages of highly adapted invertebrates. While this group is the focus of much conservation attention, available knowledge overwhelmingly reflects descriptive studies, and there have been few experimental investigations of factors affecting distribution, composition and abundance.

This chapter describes a randomised block experiment in which subsidies of food and leaf litter were manipulated over a nine week period at two sites in the River Usk Special Area of Conservation, Wales (UK). Food and leaf litter subsidies were expected to have positive effects on beetle numbers, whilst distance from the water's edge was expected to have negative effects. Over 1600 beetles were recorded of 16 species, including six ERS specialists; *Bembidion atrocaeruleum* contributed over 95% abundance. Principal components analysis of the pooled beetle data with general linear models revealed that local manipulation of food subsidies and leaf litter had no effect on carabid assemblage at the plot scale. By contrast, variations between sites, seasonal survey times and distance from water produced increasing gradients in species richness and beetle abundance, the latter largely reflecting effects on *B. atrocaerleum*. The increases in beetles with increasing distance from the water's edge probably reflected varying preferences by species for different relative humidity. These data show how larger-scale effects among reaches and through seasons subsume patch-scale resource effects on ERS beetles. One implication is that riparian habitat restoration for this group should occur at scales large enough to influence reach-scale functional responses. Marked dominance among the specialists by one species may indicate declining overall habitat suitability for ERS specialists over timescales longer than the experiment.

Key words: Beetle, *Bembidion*, Exposed Riverine Sediment, Food Subsidy, Habitat Manipulation, Leaf Litter, Reach Scale, Regulation, River Usk.

6.1 Introduction

An enduring theme throughout this thesis has been that natural influences on river ecosystem function, particularly those of discharge patterns and habitat character, have been modified through engineering, abstraction, pollution, regulation and climate change (Poff *et al.* 2007). The riparian zone is particularly sensitive, for example where exposed riverine sediments (ERS) support assemblages of highly adapted invertebrates (Bates *et al.* 2007b; Bates *et al.* 2009; Capon *et al.* 2013). The cobbles, gravels and sands within the fluvial channel that are exposed above a river's typical base flow, such as point and lateral bars, and bare islands (*Figure 2.1*), support their own specialist fauna (Bates and Sadler 2005). Particularly for key groups such as beetles, ecological changes accompanying flow regulation and habitat modification, may supplant specialist fauna with more ubiquitous species (Chapter 5), reduce abundance and limit diversity (Greenwood and McIntosh 2010; McCluney and Sabo 2012).

Effects on riparian organisms of altered flow pattern and habitat may be further compounded by changes in exchange of matter and energy between the river and the riparian zone, for example, in the form of subsidies of emerging insects or transported organic matter (Paetzold and Tockner 2005; Paetzold *et al.* 2006). In zones of ERS, drifting, stranded and emergent aquatic arthropods provide prey to riparian predators, including ERS specialist Carabidae, within a defined 'activity zone' close to the water's edge (Bates and Sadler 2005; Bates *et al.* 2005; Sadler *et al.* 2006; Paetzold *et al.* 2008; Henshall *et al.* 2011). Receding river levels not only reduce habitat and faunal heterogeneity but they might also reduce the pulsed food subsidies on which riparian predators depend (Corti and Datry 2012; Datry *et al.* 2012). Carabidae decline in numbers as aquatic prey decline, indicating reliance on these wider prey sources (Paetzold *et al.* 2006) and there is evidence also of preference for terrestrial prey particularly early in the season (O'Callaghan *et al.* 2013a).

In addition to prey abundance, river flows also affect subsidies of organic material such as woody debris and drifting leaf litter which can have a positive influence on carabid abundance (Ruggiero *et al.* 2009). Effects might reflect indirect environmental changes caused by litter, and there is evidence of the positive effect of micro-habitat wetness on beetle abundance (Henshall *et al.* 2011). Effects might also occur indirectly through interactions with prey abundances.

While the effects of flow changes, habitat modification and resource subsidies on specialist ERS beetles have been the focus of much conservation attention, available knowledge overwhelmingly reflects descriptive studies, and there have been few experimental investigations of factors affecting distribution, composition and abundance (e.g., Sadler *et al.* 2006). Only in a few cases have investigators manipulated food subsidies (e.g., artificially reduced or increased aquatic prey density) (Paetzold *et al.* 2006; Henshall *et al.* 2011; Hoekman *et al.* 2011), and in even fewer cases have wetness regimes or litter subsidies been manipulated in factorial experiments. This chapter describes a habitat manipulation experiment to investigate whether enhanced food availability, leaf litter and distance from water influenced the micro-spatial distribution of ERS specialists during a period of stable, low discharge. A randomised block design was used to provide ERS specialists with a range of food and leaf litter subsidies within the activity zone to emulate the effects of local fluctuations delivered by fluctuating river flows. It was hypothesised that food and leaf litter subsidies should have positive effects on beetle numbers, whilst distance from the water's edge was expected to have negative effects.

6.2 Methods

6.2.1 The Study Area

The experiment was carried out along the Usk river system, and the study area has been described elsewhere (Chapters 1 and 3). Manipulation was undertaken at the most upstream and downstream sites in the study area, Sites 1 and 6, respectively (*Figure 6.1*). During the preceding three years, these two sites had the most resilient assemblage of ERS specialist Carabidae despite declining availability of exposed sediments.

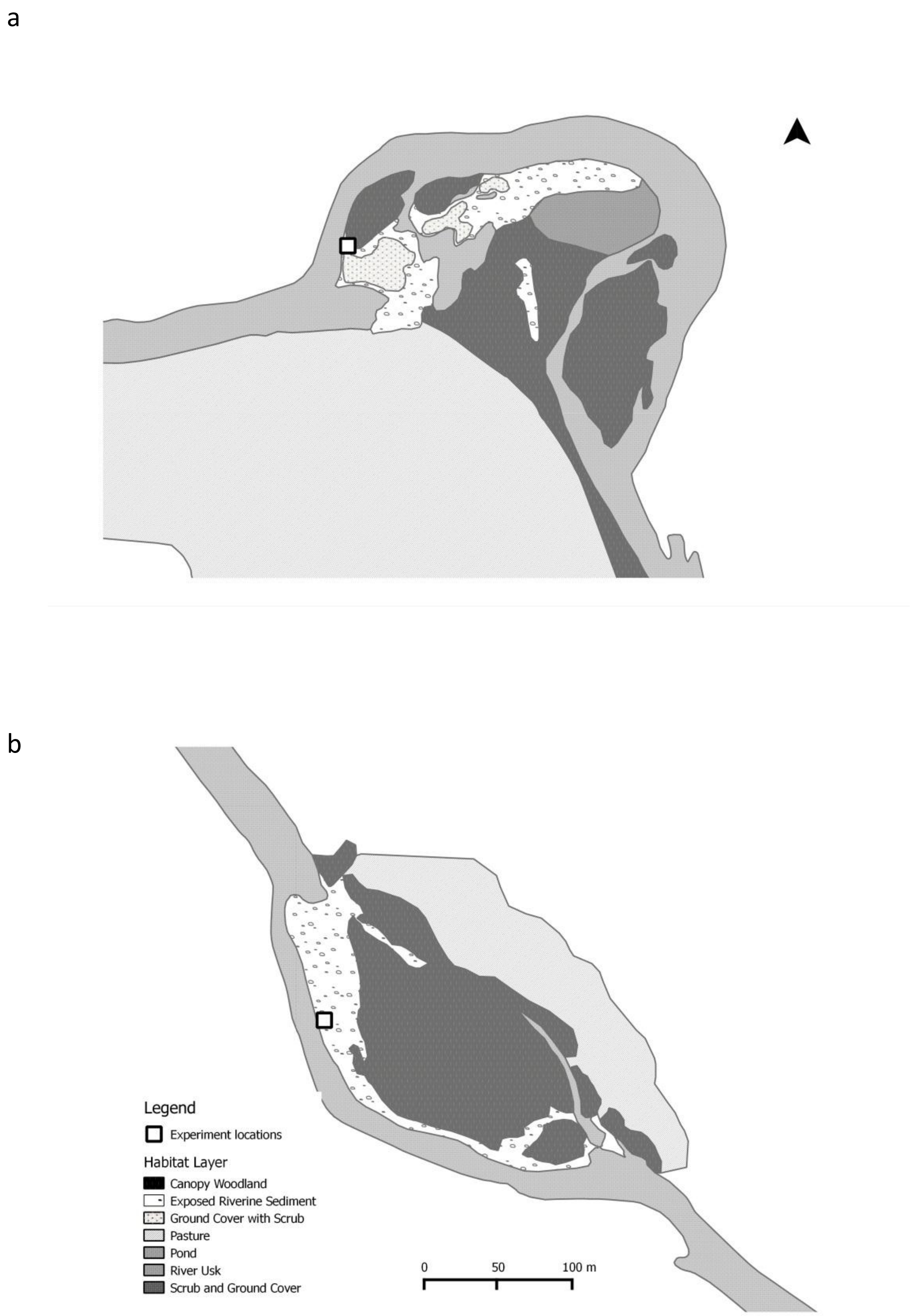


Figure 6.1 Experiment locations at a) an upstream site (Site 1, SO 09962518), and b) a downstream site (Site 6, SO11462425), in a series of six ERS sites on the River Usk in 2013.

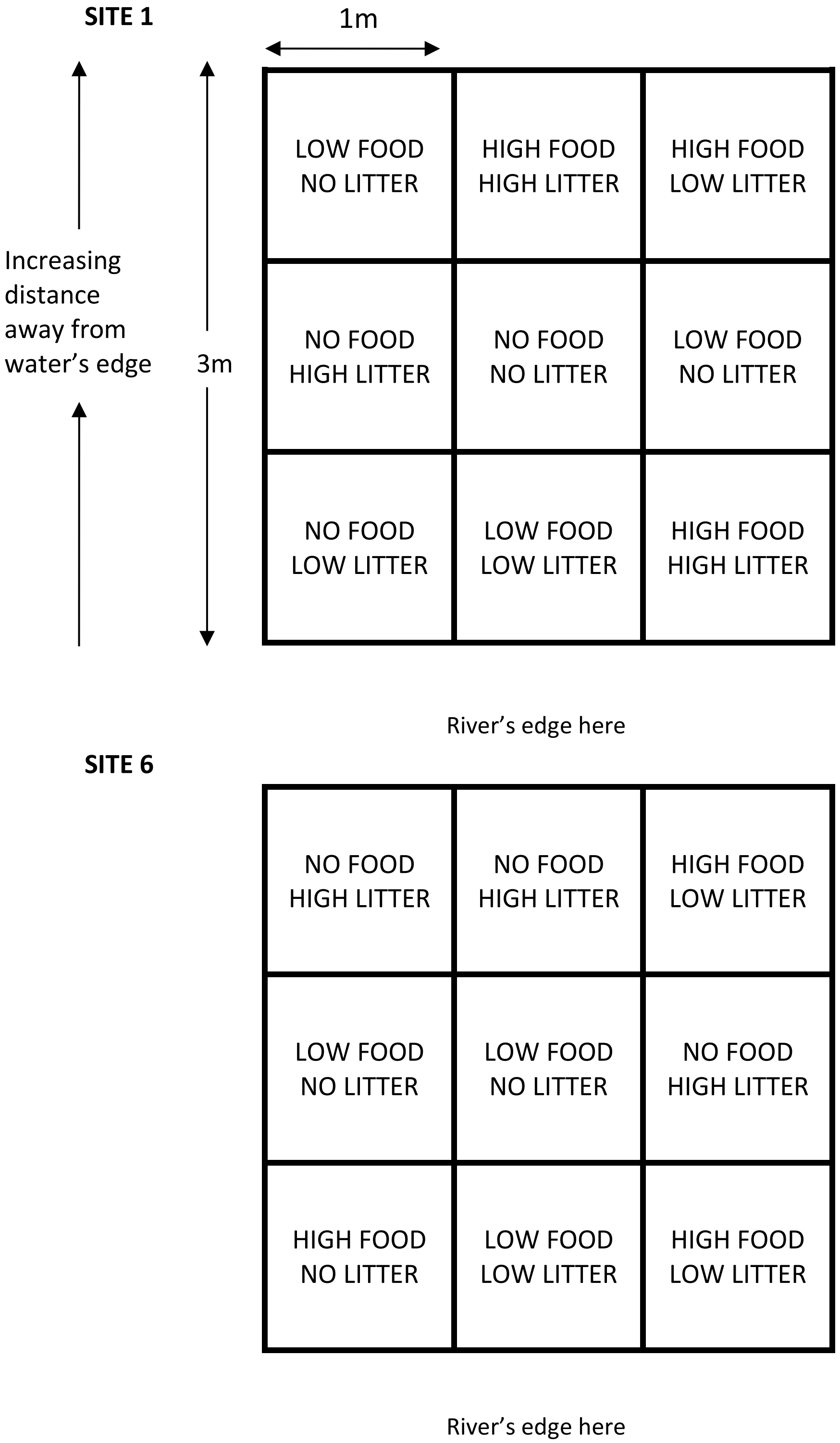
6.2.2 *Experimental Design*

A randomised block design was established on each of Sites 1 and 6 in June 2013. Experimental plot locations were established in the activity zone adjacent to the water's edge. Each plot consisted of nine cells of 1 m^2, marked by a string grid anchored with cobbles on site, treated with varying subsidies of aquatic insects (chironomid larvae) and leaf litter. Dried chironomid larvae, sourced commercially, were used as a suitable insect subsidy (Hering and Plachter 1997; Henshall *et al.* 2011) loaded at 2.5 g (low) to 5 g (high) per square metre grid cell. Terrestrial leaf litter was sourced from within the study sites and loaded 100 ml (low) to 200 ml (high) per square metre grid cell, measured using a 100 ml beaker. In each case, insect and leaf litter subsidies were estimated to emulate likely cover and inputs along the shoreline. Cells of 1 m^2 were considered suitable size to capture effects on the micro-spatial distribution of ERS specialist Carabidae based on other studies (Bates *et al.* 2005; Bates *et al.* 2007b). Combinations of food and leaf litter, or lack of thereof, were assigned completely randomly to each cell, based upon three assignments of no, low and high food or leaf litter paired randomly for each cell in each grid (*Figure 6.2*).

Some factors were outside experimental control because of fluctuations in river discharge, for example distance of the treatment plots from the wetted river margins. Accordingly, each row in the experimental block was recorded as being 0-1 m, 1-2 m and 2-3 m from the water's edge (*Figure 6.2*) during each weekly sampling event. It was expected that fluctuating river discharge introduced uncontrolled pulses of leaf litter and, presumably, food subsidies, to the semi-inundated cells, but these effects were considered part of the overall experimental design and treated as such in analysis (see below).

6.2.3 *Beetle Collection*

Each plot was visited weekly for nine weeks. During each visit, each cell was searched destructively in an effort to collect every carabid present using a hand rake and an aspirator. Each sample, from each cell, on each site, during each sample visit, was collected in a separately labelled vial containing 9:1 water and ethylene glycol plus



SITE 1

LOW FOOD NO LITTER	HIGH FOOD HIGH LITTER	HIGH FOOD LOW LITTER
NO FOOD HIGH LITTER	NO FOOD NO LITTER	LOW FOOD NO LITTER
NO FOOD LOW LITTER	LOW FOOD LOW LITTER	HIGH FOOD HIGH LITTER

River's edge here

SITE 6

NO FOOD HIGH LITTER	NO FOOD HIGH LITTER	HIGH FOOD LOW LITTER
LOW FOOD NO LITTER	LOW FOOD NO LITTER	NO FOOD HIGH LITTER
HIGH FOOD NO LITTER	LOW FOOD LOW LITTER	HIGH FOOD LOW LITTER

River's edge here

Figure 6.2 Design of completely randomised block. Treatments assigned to each cell were assigned randomly. River's edge represented 0 m distance, with each row successively 0-1 m, 1-2 m and 2-3 m distant from the water.

ethanol. Surface cobbles were replaced in each cell following each sample, and the food and leaf litter subsidies were refreshed at each sample visit.

All beetles were subsequently identified to species level using Luff (2007). The experiment ended when, following the ninth visit, the plots were totally inundated by encroaching river levels.

6.2.4 Statistical Analysis

For each experimental cell in each plot on each week, data recorded included species richness, beetle abundance and abundance per species per cell. Larvae were not identified to species and were instead grouped as a single quasi-species "larvae", and treated as an ERS specialist. Beetle data (counts per species) were first treated by principal components analysis on the matrix of correlations among species to provide a principal component score that represented overall changes in composition. Species richness, beetle abundance and PC scores, as dependent variables, were related to the experimental factors using general linear models. Independent factors were site (spatial variation), time (temporal variation, i.e., week of sampling visit e.g., 1, 2, 3 etc.), food subsidy (high = 2, low = 1, none = 0) and leaf litter (high = 2, low = 1, none = 0), with distance from water treated as an uncontrolled covariate and independent factor. The influence of distance from water was additionally investigated independently of other factors. Least squares means were plotted and the best fitting models identified using Akaike's Information Criterion (AIC), given by the equation

$$n * \ln(\sigma^2) + 2(k + 1),$$

where n is sample size, k is the number of variables modelled and σ^2 is the variance calculated from the Adjusted Sum of Squares/n. The lowest AIC value indicated the best fitting model.

Due to the high frequency of low abundances and singletons, abundances of each species were transformed by Log(n+2) prior to further analysis. All statistical analyses were completed using Minitab 16®, with Akaike's Information Criterion calculations completed in Excel.

6.3 Results

Moderate river fluctuations over the experiment led to some inundation effects: during Week 2 at Site 1, the 0-1 m cells were semi-inundated, whilst at Site 6, the 0-1 m cells were wholly inundated and 1-2 m cells were semi-inundated, so these cells were not available for sampling. During Week 3, no sampling was completed due to poor weather.

6.3.1 Beetle Abundance, Richness and Community Composition

Following eight sample visits during the nine week experiment, 1,653 beetles of 16 species were recorded, including seven ERS specialists (Fowles 2004). Principal components analysis revealed three principal components, cumulatively explaining 17.6%, 28.7% and 37.6%, respectively, of spatio-temporal variation in abundance per species (*Table 6.1*). Eleven species dominated the PCs, of which six were ERS specialists. *Bembidion atrocaeruleum* (Stephens) accounted for 91.6% of all individuals, though this dominance was controlled in the PCA by the log(n+2) transformation (*Figure 6.3*, *Table 6.1*). Five species increased in abundance on PC1, including three generalist species, *Synuchus vivalis* (Illiger), *Pterostichus vernalis* (Panzer) and *Paranchus albipes* (Fabricius), as well as two ERS specialists, *B. punctulatum* (Drapiez) and larvae. In PC2, three species increased in abundance, including two ERS specialists, *B. prasinum* (Duftschmid) and *B. decorum* (Zenker in Panzer), and the generalist *Agonum muelleri* (Herbst). Similarly in PC3, three species increased in abundance, including two ERS specialists, *B. atrocaeruleum* and *B. tibiale* (Duftschmid), and the generalist *B. tetracolum*.

General linear models revealed that experimental subsidies of food and leaf litter, as well as distance from water, produced no detectable effects on any of the recorded beetle attributes (*Table 6.2*). By contrast, differences between sampling season (sample visits) and experimental plots (Site 1 *v* Site 6) had highly significant effects. For example, species richness increased during the survey season, and between Sites 1 and 6 (survey season: $F_{7, 141} = 5.84$, $p < 0.001$ and between sites: $F_{1, 141} = 11.95$, $p < 0.001$, R^2adj' = 36.84%), as did beetle abundance (survey season: $F_{7,\ 141}$ = 19.56, $p < 0.001$ and between sites: $F_{1,\ 141}$ = 35.57 $p < 0.001$, R^2adj' = 64.89%) (*Figure 6.4*). PC1, representing increasing abundance of three generalist species and two ERS specialists, increased during the survey season ($F_{7,\ 141}$ = 2.22, $p < 0.05$, R^2adj' = 8.67%), whilst PC3, representing two ERS specialists, including the most abundant species and one generalist species, increased during the survey season and between Sites 1 and 6 (survey season: $F_{7,\ 141}$ = 4.52, $p < 0.001$ and between sites: $F_{1,\ 141}$ = 7.81 $p < 0.01$, R^2adj' = 31.75%). PC2 showed no increases during the survey season or between sites.

Investigating the effects of distance from water's edge independently, species richness, beetle and abundance and PC3 all increased with increasing distance ($F_{13,\ 141}$ = 2.13, $p < 0.05$, R^2adj' = 9.46%, $F_{13,\ 141}$ = 5.12, $p < 0.001$, R^2adj' = 27.52%, and $F_{13,\ 141}$ = 2.6, $p < 0.01$, R^2adj' = 12.87%, respectively) (*Table 6.3*, *Figure 6.5*). There were no significant responses by PC1 or PC2.

Akaike's Information Criterion values revealed that beetle abundance and species richness responded most strongly to the overriding environmental effects of season, site and distance from water's edge, whilst PC3 responded more strongly than PC1 (*Table 6.4*). Neither PC1 nor PC3 responded to this factor, suggesting that PC3, which was dominated by the most abundant species, was also influential in the response by beetle abundance.

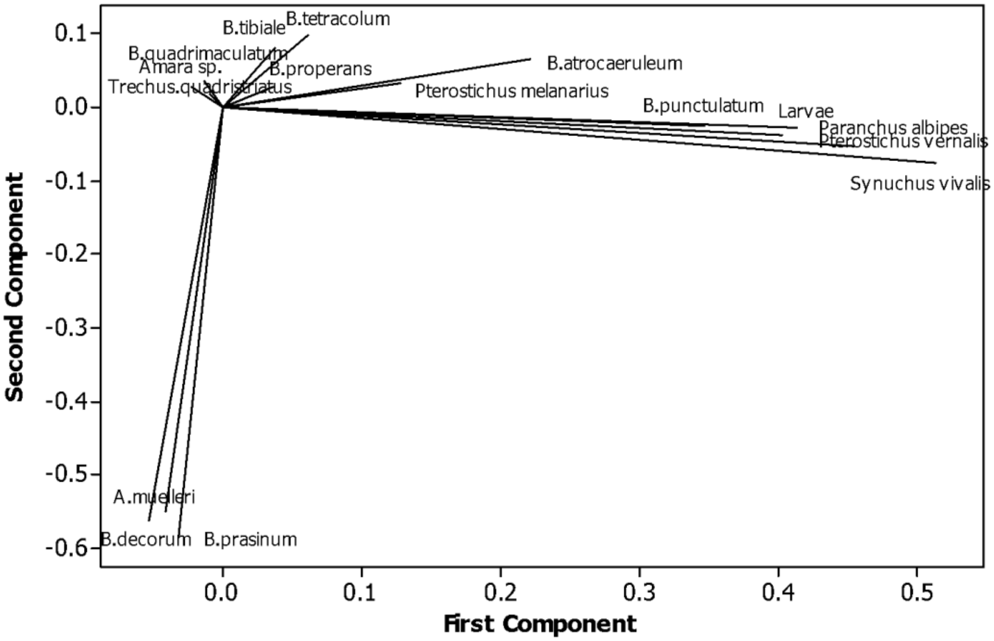


Figure 6.3 Species distribution on the first two principal components of species abundances during a nine week experimental habitat manipulation on two ERS sites in the Usk river system, Wales (see *Table 6.1* for loading values).

Table 6.1 Loading values of dominant beetle species (shaded) on three principal components derived from correlation among their abundances (see *Figure 6.3* for graphical display). ✓ indicates ERS specialist.

	PC1	PC2	PC3
Eigenvalues	2.81	1.77	1.43
Cumulative proportion	17.60%	28.70%	37.60%
B.atrocaeruleum ✓	0.221681	0.065987	0.553113
B.decorum ✓	-0.05386	-0.56343	0.036921
B.prasinum ✓	-0.03225	-0.58558	0.14898
B.punctulatum ✓	0.345964	-0.02503	-0.12329
B.tetracolum	0.060758	0.097734	0.522713
B.tibiale ✓	0.037143	0.080123	0.488831
B.quadrimaculatum	-0.01313	0.034554	0.047805
B.properans	0.036131	0.026632	0.062947
Paranchus albipes	0.401987	-0.0382	-0.04214
A.muelleri	-0.04116	-0.55104	0.078572
Pterostichus melanarius	0.127861	0.031729	-0.00396
P.vernalis	0.454063	-0.05379	-0.19228
Synuchus vivalis	0.513501	-0.07692	-0.19723
Trechus quadristriatus	-0.00937	0.018319	-0.10144
Amara sp.	-0.02277	0.027804	-0.0548
Larvae ✓	0.41301	-0.0273	0.199361

Table 6.2 GLM showing variations in carabid assemblage structure following a nine week experiment on two ERS sites, manipulating food and leaf litter, with distance from water an uncontrolled covariate. Significance levels indicate * p < 0.05, ** p < 0.01 and *** p < 0.001. See *Table 6.4* for AIC values and *Figure 6.2* for least squares mean plots.

	Species richness	Beetle abundance	PC1	PC2	PC3
Distance from water	NS	NS	NS	NS	NS
Time	***	***	*	NS	***
Site	***	***	NS	NS	**
Food	NS	NS	NS	NS	NS
Leaf Litter	NS	NS	NS	NS	NS

Table 6.3 GLM showing the influence of distance from water's edge on variations in carabid assemblage structure following a nine week experiment on two ERS sites. Significance levels indicate * p < 0.05, ** p < 0.01 and *** p < 0.001. See *Table 6.2* to compare the influence of this factor with other factors. See *Table 6.4* for AIC values and *Figure 6.5* for least squares mean plots.

	Species richness	Beetle abundance	PC1	PC2	PC3
Distance from water	*	***	NS	NS	**

Table 6.4 Akaike's Information Criterion values following GLM and ANOVA of carabid assemblages influenced by factors during a nine week habitat manipulation experiment on two ERS sites on the Usk river system, Wales, UK. Lowest AIC values indicate the strongest effect, ranked for a) beetle abundance, b) species richness, and c) species principal components.

		AIC value	**Factor**
a	Beetle abundance	-383.36	Time Site
		-229.82	Distance from water
b	Spp richness	-64.05	Time Site
	Spp richness	6.93	Distance from water
c	PC3	-4.14	Time Site
□□PC3□53.84□Distance from water	PC3	53.84	Distance from water
	PC1	131.33	Time

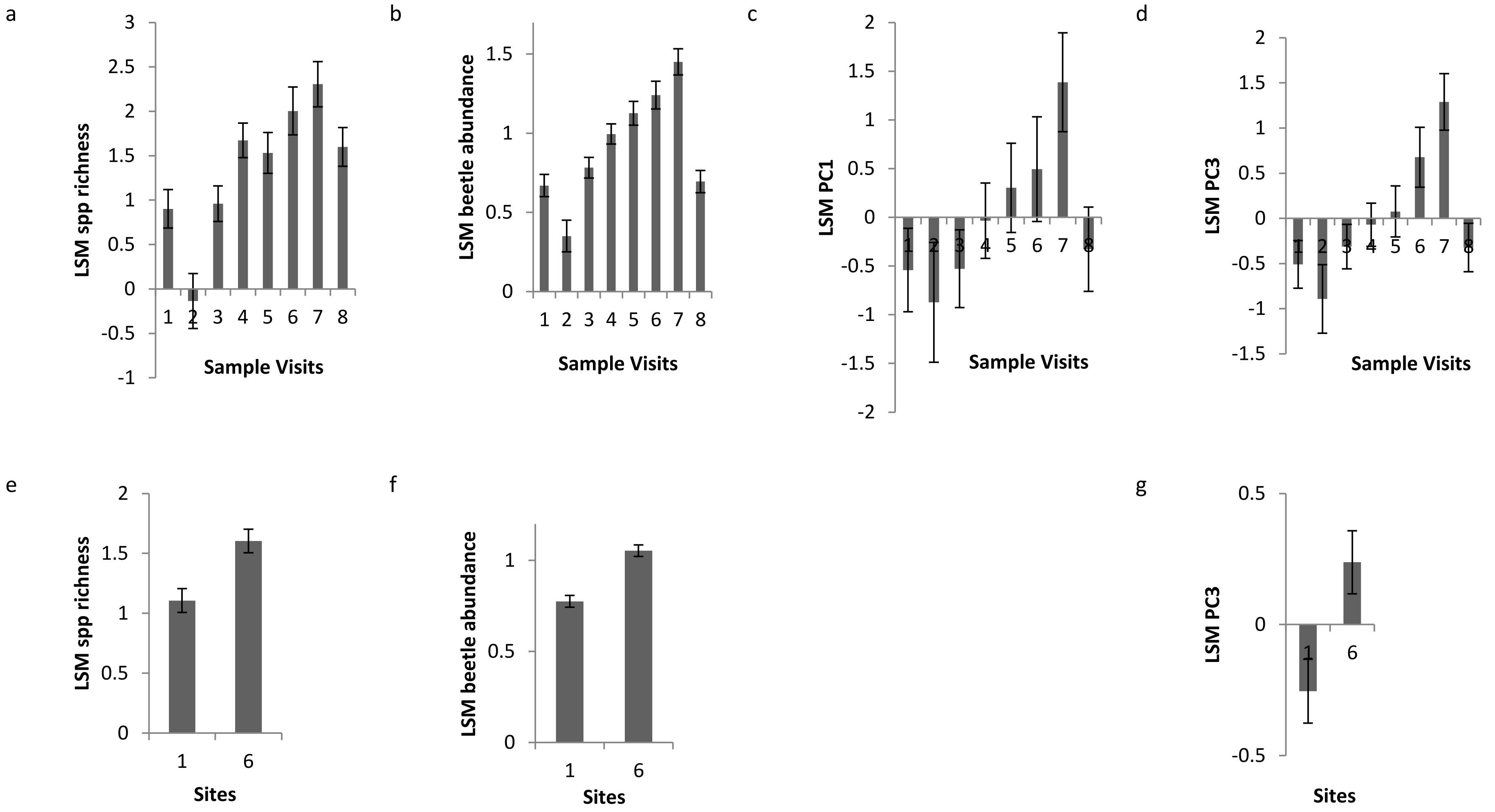


Figure 6.4 Seasonal (sample visits) and inter-site gradients in carabid assemblage structure during a nine week habitat manipulation experiment on two ERS sites in the Usk river system, Wales, UK, plotting least squares means (LSM) and standard error. a) to d) seasonal responses by species richness, beetle abundance, PC1 and PC3, and e) to g), inter-site responses by species richness, beetle abundance and PC3, respectively.

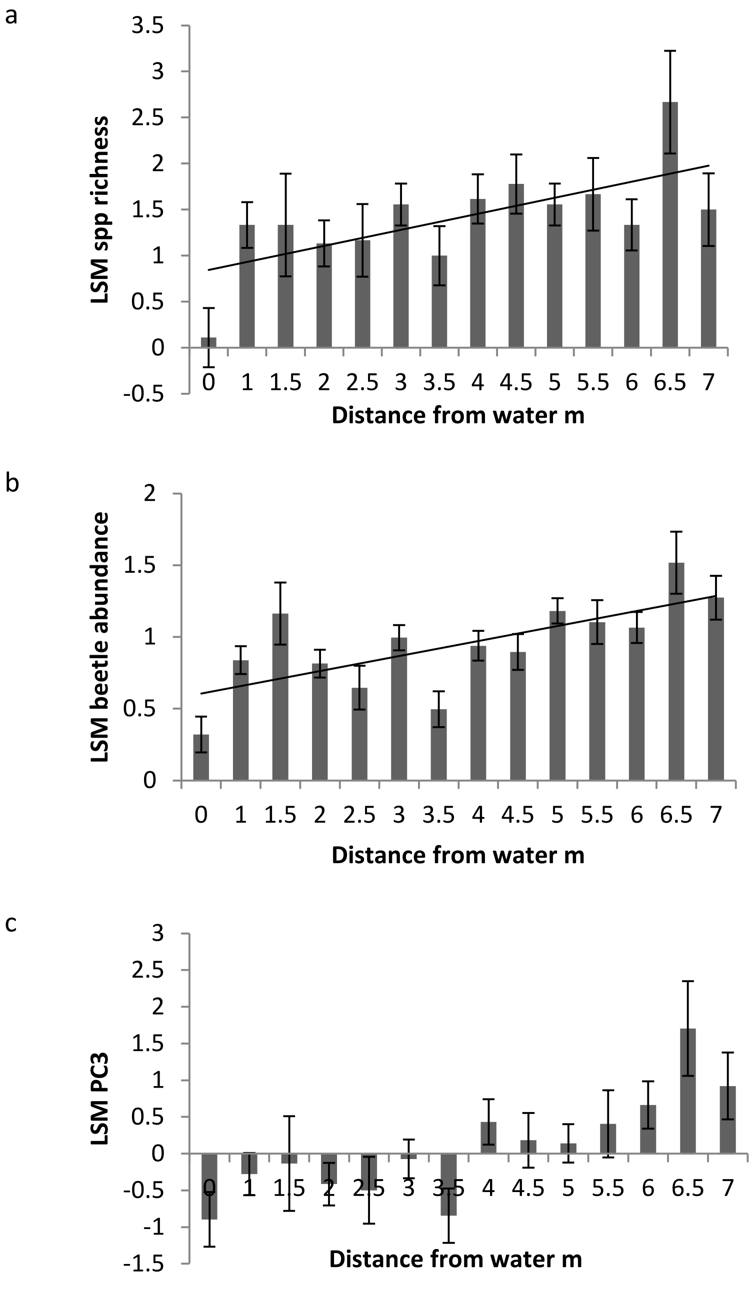


Figure 6.5 Gradients in a) species richness with fitted trend line, b) beetle abundance with fitted trend line, and c) PC3 score with distance from water, plotting LSM (and standard error), during a nine week habitat manipulation experiment on two ERS sites in the Usk river system, Wales.

6.4 Discussion

This chapter examined the hypothesis that food and leaf litter subsidies had positive effects on beetle numbers, whilst distance from the water's edge was expected to have negative effects. Insect distribution patterns are influenced by spatio-temporal patchiness of resources and distance between patches, and this, coupled with species' dispersal ability, influences population dynamics (Compton 2002). In this study, the micro-distribution of ERS specialists manifested no response to a within-site experimental manipulation of food and leaf litter. By contrast, assemblage composition, in particular species richness and beetle abundance, as well as the abundance of two species components, increased strongly in response to the much larger effects of spatial separation between experimental sites, seasonal sequence of sample visits and distance from the water's edge. Specialists of ERS were resilient in these spatial and temporal responses, though the strongest responses overall were by the abundance of generalist species, which suggests a possible short term succession effect (Chapter 5). Whilst its influence was masked by the larger effects of space and time, distance from the water's edge affected the overall assemblage structure, with species richness, beetle abundance and the most abundant species, *B. atrocaeruleum*, increasing with distance. Sediment wetness, which moderates surface temperatures, as well as proximity to the water's edge, where food and leaf litter subsidies are delivered, are each known to exert a positive influence on the distribution of ERS specialists (Luff 2007; Lambeets *et al.* 2008b; Henshall *et al.* 2011; O'Callaghan *et al.* 2013a). Different ERS specialists, however, are known to exhibit different relative humidity preferences (Andersen 1985a), so a distribution gradient moving away from the most saturated, and humid, sediments, such as was recorded in this experiment, might have been expected (Bates *et al.* 2007b). However, by exhibiting an increase in species richness and beetle abundance, with increasing distance from water, it contradicted the negative effect predicted.

Sediment wetness was not investigated in this study. Anecdotal observations during the experiment were that the Site 1 plot, which was on a flat location, was noted to have dry, coarse underlying shingles throughout the experimental period. The plot at Site 6, whilst gently sloping, had finer, damper underlying shingles than the Site 1 plot.

By Week 7, the underlying shingles at Site 6 were also dry. Thus, whilst during the experiment species richness, beetle abundance and the *B. atrocaeruleum* component each increased as the survey season progressed, the underlying sediments dried out. These same dependent variables also increased with distance from the water's edge, which suggested that a phenological factor may have been influential, such as seasonal abundance patterns of different species. For example, the later season increase in *B. atrocaeruleum* and larvae (PCs 1 and 3) may have been influenced by the dominance of *B. atrocaeruleum*, a species known to reproduce during spring with a peak of larvae and teneral adults during July to August (Bates *et al.* 2006).

Whilst experimental manipulation of food pulses and leaf litter provoked virtually no significant response by the specialist ERS assemblage, it was undertaken in the knowledge that *Bembidion* abundance has been associated with availability of aquatic food subsidy (Paetzold *et al.* 2006; Henshall *et al.* 2011), that subsidy delivery is influenced by inundation events and that where river discharge is in decline, the aquatic-terrestrial nutrient exchange may decline too (O'Callaghan *et al.* 2013a). Highly mobile ERS specialists that possess a stronger avoidance response to advancing river levels (O'Callaghan *et al.* 2013a) also possess traits most likely to exploit aquatic food subsidies. Yet, during a period of prolonged, inter-annual low discharges preceding this study (Chapter 4), an effect demonstrated to exert a negative effect on assemblage composition and abundance for riparian arthropods (McCluney and Sabo 2012), the highly mobile *B. atrocaeruleum* remained highly abundant, although at a declining level each year; it was the most abundant species in this experiment. This, by comparison with the three other principal species identified, which were collectively outnumbered by *B. atrocaeruleum* by a factor of 126:1, reflected its ubiquitous ecology among ERS specialists and its readiness to disperse between ERS habitats (Bates *et al.* 2006), making it independent of local experimental and spatio-temporal effects. Its abundance during this experiment might also have reflected the declining habitat suitability for other ERS specialists reported in Chapter 4, and increasing habitat homogeneity during consecutive summer periods of low river discharge investigated in Chapter 5.

Whilst the effects of experimental habitat manipulation were not apparent, it is possible that the general availability of food subsidy within the 9 m^2 plots may have exerted a positive effect on abundance of *B. atrocaeruleum*; however, no comparative control studies were run to test this. It is possible that the food and leaf litter manipulations affected a wider food web. Long term food manipulation within the riparian zone has been shown to influence aquatic-terrestrial nutrient transfer through detrivores and higher order predators such as Coleoptera and Hymenoptera (Hoekman *et al.* 2011). Also, ERS specialists are known to respond to environmental factors such as distance from water, local elevation (Bates and Sadler 2005) and lateral distribution of ERS specialists in response to laterally graded factors such as surface temperature, humidity, inundation frequency, food subsidies, vegetation cover and sediment sorting (Bates *et al.* 2007b),

It is possible that without prior testing of response thresholds by ERS specialists, experimental design provided insufficient food and leaf litter subsidies, and habitat manipulation would have benefited from a range of spatial trial runs prior to commencing the experiment (Talley 2007). The weekly sample periods may have been too long or too short; beetle responses may have peaked prior to or after a one week threshold. The beetles tended to occur in patches within the 1 m^2 cells (*pers. obs.*), suggesting that a smaller grid design might have detected micro-spatial distribution patterns (Bates *et al.* 2007b). During each sample visit, each cell was searched destructively and then reconstructed by returning the displaced sediments within each cell, effectively resorting and redistributing them on a 1 m^2 scale. This ‘reset’ each cell or each sample grid back to a ‘primary succession’ state devoid of beetles but supplied with food and leaf litter. Under these conditions it is possible that any manipulation effects would arise only over longer time periods than the intervals between samples, relying upon the regularity of environmental disturbance events that trigger dispersal by ERS specialists, to supply colonising beetles to these localised experimental ‘sinks’. The experiment may have been caught in a paradox wherein the environmental event required to trigger dispersal, i.e., inundation by rising river levels, was not available during successive years of low discharge. Such an event would have submerged the experimental plots, thereby destroying the experiment. An experimental modification to overcome this would have been to construct floating experimental plots.

It is possible that the 1 m^2 grids were too small to differentiate an effect of food subsidy and leaf litter on distribution of highly mobile fauna. Edge effects between grid edges might also have been significant if highly mobile fauna moved arbitrarily between cells; this effect was not studied, for example using a mark-release-recapture study. The overriding influential effects of time and site were of a much larger scale than this, requiring much larger food and leaf litter manipulation to have been undertaken to offset these background effects. The richness and abundance gradient between sites suggested that habitat manipulation across an entire site would have been the appropriate scale to conduct the experiment. No measures were made of surface temperatures, insolation, sediment size or relative humidity, though these factors are known to influence beetle distribution (Andersen 1985a, b, 2006; Andersen 2011a) and have been recommended for further study (Bates and Sadler 2005).

Receding river flow and encroaching vegetation across ERS, reported in Chapter 4, indicated a declining interaction across the aquatic-terrestrial interface. Whilst the results of this experiment indicated that effects on the spatio-temporal abundance and distribution of ERS specialists are scale-dependent, they also suggested that riparian functionality declined during prolonged low river discharge, which was a large ‘background’ effect. The high abundance of a ‘generalist specialist’ such as *B. atrocaeruelum* by comparison with other ERS specialists, may have underlined this effect, where ERS patches declined in suitability for specialists as they became more generic in response to low flows. This emphasised findings of other authors (O'Callaghan *et al.* 2013b), in recognising the functional value of ERS specialist Carabidae in understanding the ecological relationship between rivers and their floodplains, where ERS specialists are mediators of nutrient exchanges (Paetzold and Tockner 2005) and changing ERS specialist assemblages indicate changing riparian health.

7 General Synthesis

7.1 Research Findings and Their Implications

The overriding aim of this study was to enhance understanding of environmental change within river systems, using ERS and their specialist carabid beetles as study subjects. Thus it was a departure from previous studies of ERS and Carabidae, which have focussed on the conservation needs of the organisms (e.g., Bates *et al.* 2007) but have only recently, and modestly, turned their focus towards functional studies of ERS within riparian ecosystems (e.g., O'Callaghan *et al.* 2013b).

Using a three year investigation, preceded by a test of appropriate sampling techniques and succeeded by a habitat manipulation experiment, the study addressed the dearth of multi-year studies on ERS, or appropriate sampling techniques for multi-site and multi-year studies. The River Usk, which is designated as a Special Area of Conservation and also as a Site of Special Scientific Interest, possessing numerous ERS in its upper and middle reaches, was a suitable area to study spatial and temporal factors influencing specialist beetles. With frequently impounded headwaters and regular water abstraction both for regional drinking water and for amenity supplies to the Monmouthshire and Brecon Canal, there is a need to understand the river's long term ecological status in a changing climate. This study contributed to that understanding by undertaking studies of potentially vulnerable and ecologically responsive fauna on ERS during successive periods of low river discharge.

The field component commenced with an examination of sampling techniques suitable for providing a resilient and representative dataset of Carabidae. The technique needed to generate proportionally representative assemblages of ERS specialists in a rapid and even-handed manner. It needed to permit the surveyor to respond to dynamic change on ERS, for example fluctuating river levels, which are tracked by ERS specialists at the shoreline. In order to collect all samples during 'the same' diurnal conditions, the technique needed to permit rapid, quasi-simultaneous samples to be taken across numerous locations on geographically separate patches sampled repeatedly; and it needed to accumulate sufficient volumes of samples to improve statistical rigour. Evidence in the literature suggested that hand searches and pitfall traps were the most widely used techniques. Results from a modest comparative study found timed hand searches to provide a more representative assemblage, with a higher proportion of ERS specialists, than pitfall traps. The timed hand search technique was modified by the use of a small hand rake, rather than painstakingly turning over stones by hand, which permitted rapid and even-handed exposure of the sediment profile where the beetles lived; and it was standardised by regularised sample periods.

This technique provided reliable data during a longer three year multi-site and multi-visit survey of carabid beetles on ERS, during a period of successive, prolonged summer river discharge stability. Using data collected on local habitat character, local character was found to play a negligible role in influencing beetle assemblage structure and distribution, with temporal and spatial availability of ERS playing a much stronger role, potentially influenced by river discharge. The local habitat variables recorded for the three year study were based on previous approaches (Sadler and Bell 2000; Sadler *et al.* 2006) but they proved to be ineffectual in understanding beetle assemblage structure and distribution in response to environmental change. These variables may be appropriate in studies of ERS hydro-geomorphology and terrestrialisation (Bornette and Amoros 1996; Gergely *et al.* 2001; Bertoldi *et al.* 2011; Gurnell *et al.* 2012) but results from this study suggested that the influence of habitat and vegetation dynamics on ERS might more reliably be measured at the reach scale.

The increasing terrestrialisation of ERS raised the possibility that beetle assemblage structure might change accordingly, shifting from a more specialised to more general suite of species each year. Despite a dearth of multi-year studies of carabid beetles and ERS, results reported in Chapter 5 suggested that this three year study was too short to detect any definite signs of assemblage succession. Mean Individual Biomass, in combination with species richness and abundance patterns, did not reveal any significant inter-annual trends towards a more generalist assemblage. It had been used by other authors to record beetle assemblage succession between regional forests managed at successive plagio-climaxes but had not until this study been used on ERS or during a multi-year study. Exposed riverine sediments change and terrestrialise relatively rapidly, therefore it was hoped that changing MIB would provide an effective marker for assemblage succession tracking this dynamic. Results were inconclusive, suggesting that despite the relatively rapid terrestrialisation that ERS might experience, assemblage succession on ERS needs investigating during a longer period than three years.

In Chapter 6, further efforts to influence local habitat character, through experimental manipulation of food and leaf litter subsidies, were ineffective, with assemblage structure responding to the larger effects of inter-site variation and seasonal beetle abundance. Localised distance from the water's edge was influential on beetle distribution, reflecting species' preferences for different local humidity levels, which are affected by sediment wetness.

Overall, results showed that specialist carabids responded to environmental change at a larger scale than within-patch. Previous studies have demonstrated within-patch responses to disturbance, such as inundation (Bates *et al.* 2006) and food availability (Paetzold *et al.* 2006; Henshall *et al.* 2011) but this is smaller in scale and duration than environmental change such as prolonged or successively low river discharge and vegetation encroachment (terrestrialisation of ERS). Insects also respond to diurnal patterns in insolation, air temperature and precipitation but these are reversible factors triggering ephemeral responses rather than potentially irreversible changes to physical structure and ecological availability of ERS.

Other studies in the UK have focussed on relatively unmodified, unregulated rivers or stretches of rivers (e.g., Sadler *et al.* 2006; Bates *et al.* 2009; O'Callaghan *et al.* 2013). This study focused on a river regulated by impoundment, abstraction and entrainment (Chapter 1), experiencing successive low summer discharge and thereby differentiating findings from those applied to ERS in a comparatively unmodified river. Studies included investigations of intra- and inter-annual, within and between site investigations. No significant inundation events, and therefore significant re-distribution or sorting of sediments, occurred. Absence of environmental perturbations that are essential to the definition of ERS, and the exposure of river bed sediments, introduced the possibility of atypical species distribution patterns and assemblages. Four principal ERS specialist species were resilient in the three year assemblage, with the most abundant species *Bembidion atrocaeruleum* (Stephens) declining annually whilst the other three increased annually. This was suggestive of an overall homogenisation of the ERS environment, accompanied by a magnification of conditions suitable for three species, for example tracking freshly exposed sediments adjacent to the water's edge as river flow retreated.

Although it was not referred to in this study, where low discharge events fall below the Q10 percentile (the river level at which only 10% of the annual daily mean flow are lower than this, so that 90% are above this threshold), this can cause direct riparian mortality and habitat destruction, depending upon the number of days per year that this level is exceeded (Sadler *et al.* 2006). Vegetation-mediated landforms, where plants behave as ecosystem engineers by trapping suspended sediment, in turn favouring more plant colonisation and land formation in a positive feedback loop (Bertoldi *et al.* 2011; Gurnell *et al.* 2012), may become a more frequent dynamic within low flow rivers experiencing high and ecologically damaging levels of sediment load; such as the River Usk (Larsen *et al.* 2009). This will militate against the availability and rejuvenation of ERS in such rivers and this must be set against the backdrop of declining ERS resources in the UK and Europe (O'Callaghan *et al.* 2013b).

A recurring factor in this study was the vulnerability of rivers and riparian ecosystems to anthropogenic factors altering their ecology, such as flow regulation. A literature review of environmental change within the riparian zone and on ERS in particular (Chapter 2), argued that the definition of ERS in regulated rivers may need to be less rigid because prolonged or regular periods of anthropogenic low discharge exposes more sediment than the definition recognises. Whilst ERS in naturally fluctuating rivers ideally occur above a river's natural base flow, if sediments are exposed below this for prolonged periods, these areas become essential to the survival of ERS specialists as the exposed hinterland shrinks beneath encroaching vegetation. Whilst population turnover must occur faster than habitat turnover to avoid local extinction within transient habitats, a low frequency of inundation events may reduce the availability of new ERS sites to dispersing beetles, with remaining ERS becoming increasingly terrestrial, i.e., disappearing. Source-sink population dynamics function where individuals flow from more productive to less productive environs on adjacent sites (Wilson and Thomas 2002; Bates and Sadler 2005). The obvious conclusion therefore is that where low discharge persists, accompanied by terrestrialisation of ERS patches, specialist ERS assemblages will become increasingly isolated and at risk from population crashes and localised extinction as the ERS resource diminishes. Whilst species such as the four principal species identified in Chapter 4, might persist or accumulate annually within a constrained ERS zone, this could be a temporary spike prior to a specialist assemblage crash as suitable conditions decline in the face of 'riparian squeeze' caused by land use and river regulation pressures.

Since ERS respond to river fluvial geomorphology, and, as this study has demonstrated, dependent species respond to reach-scale, annual and seasonal change, it is axiomatic that ERS cannot be managed as specific habitat types. As ephemeral habitats, their fate is tied to that of the wider river system, in particular to the intensity of the combined intensity of natural discharge, impoundment and abstraction (Guareschi *et al.* 2014). It is also axiomatic that rivers cannot be managed *in order to maintain* ERS. The Group Action Plan for River Shingle Beetles (UKBAP 1999) targeted effort at distribution studies. In follow up, conservation effort must now be targeted at landscape-scale river system intervention to maintain, and restore, ERS ephemerality. In return, the resilience of ERS and their representative Coleoptera can provide 'vital signs' of the status of river systems in response to anthropogenic stressors and restorative interventions.

The scale-based findings in this study can be set in the context of riverine faunal assemblages existing within a longitudinal river gradient, though there is more to understand about how the structure and function of a river changes along this gradient (Arscott *et al.* 2005). Apart from distinct upper, middle and lower reach assemblages influenced by the hydro-period (Reese and Batzer 2007), further elucidation is needed on how faunal communities are organised (Lambeets *et al.* 2008a; 2008b; 2009). Additional complexity is provided via lateral gradients across the terrestrial-aquatic ecotone influencing species structure and abundance within riparian communities (Arscott *et al.* 2005; Paetzold *et al.* 2008; Larsen *et al.* 2009). This relationship changes from upstream to downstream in response to changing physical factors and inundation frequency. There is uncertainty over whether changes are continuous along a gradient reflecting continuous river flow (Tomanova *et al.* 2007) or within discrete zones and discontinuous hydro-geomorphological patches affected by lateral influences (Lorenz *et al.* 1997; Thorp *et al.* 2006; Lutscher *et al.* 2007). Uncertainties may be due to the faunal groups studied, the scale at which they are studied and the study methods used.

It is likely that the ERS patches were increasingly affected by lateral influences during retreating river flow, i.e., encroaching terrestrialisation accompanied by terrestrial or generalist fauna. The thesis did not examine this phenomenon directly and, in the absence of definite indications of faunal succession, a longer time frame than three years might be required to determine lateral intrusion. Several of the habitat variables could be jettisoned in future, relying just on the extent of ground cover and adding a new habitat variable: sediment grouting, i.e., the degree to which shingles are 'grouted in' by fines deposited from terrestrial erosion upstream. This phenomenon was observed in a few locations and might affect the resistance and resilience of specialist Carabidae assemblages during prolonged low discharge, and reflecting deleterious land use change upstream.

Ideally, a longer study should incorporate all ERS within a river system, so that they are each sampled simultaneously during successive years. The fluctuation between longitudinal and lateral flows will vary along a river's length, affected by variations in sediment load, bed movements, river gradient, regulation and land use at different locations. This thesis demonstrated that ERS Carabidae respond to these changes, so, by simultaneous surveys on every site, it would be possible to characterise ERS zones and to devise ERS templates that reflect the hydro-geomorphology upstream and the land use both upstream and adjacent to the sites.

7.2 Landscape-scale Intervention

Scale-based findings contribute to the perennial debate about the appropriate scale at which to undertake system restoration (e.g., Clews *et al.* 2010). The study area was situated within the Brecon Beacons National Park, which, like all British national parks, is a Category V protected landscape (IUCN 2014). Management of these protected landscapes is guided by 12 management principles (Phillips *et al.* 2002), which include a focus on the interaction between people and the environment; social justice and good governance; management led by and for local people through cooperation; achieving enhancement as well as protection; and measuring success in terms of environmental and social outcomes. This focus provides a useful framework for the ecosystem approach to natural resource management. Yet Britain's national parks, by virtue of encompassing Britain's highest, lowest, wettest, driest, warmest and coldest places, may consequently be particularly vulnerable to the adverse effects of climate change, as will the people who live there. The landscape scale, or in the context of river systems, reach or catchment, is the appropriate scale across which to affect change that influences the distribution and resilience of ERS, ensuring that the taxonomic and functional diversity that ERS provide, is maintained. Where they occur, such as within a protected landscape, ERS provide a highly visible and, in relation to specialist fauna, relatively simple resource to monitor the state of the riparian environment and rate of environmental change. This may prove to be highly topical where protected landscapes are required to serve increasingly important roles such as freshwater reserves (Lawrence *et al.* 2011), to provide resilient, heterogeneous and reliable corridors for species dispersal (Beier and Brost 2010; Brost and Beier 2012a, b; Ruddock *et al.* 2013), and to continue to provide strategically important drinking water reserves (DCWW 2014).

7.3 Recommendations

There is a strong case to focus more research on ERS and their dependent fauna in order to develop a better understanding of the rate of environmental change, or resilience, within river systems, in response to anthropogenic stressors, and the interplay between biological and physical processes (Tabacchi *et al.* 2009). The understanding of Favourable Conservation Status of Natura 2000 sites (EC 1992) and good ecological status of freshwaters (EC 2000) can benefit from using habitat patches such as ERS, whose traits lend themselves to rapid ecological assessment and low-tech, repeatable surveillance, such as hand searches. This can be combined with geographic studies of physical resilience and land/fluvial migration, for example using digital elevation models and aerial surveillance of ERS, as well as readily available datasets such as river discharge and precipitation.

To contribute understanding of the vulnerability of river ecosystems to anthropogenic change, and the scale and direction of change, a longer term study is required of potential homogenisation of ERS and functional homogenisation of associated faunal groups as locally adapted specialist assemblages are supplanted by generalists (Clavel *et al.* 2011; McCluney *et al.* 2014; Thorp 2014). This can be undertaken at nested scales, for example studying a very large river such as the River Severn, fed by a large river such as the River Wye and a medium-sized river, such as the River Usk; and reach-scale faunal studies within these. This approach would also be appropriate to study river responses to restorative intervention.

7.4 Post Script

The three year field work generated a large dataset of over 9000 beetles and 28 species during three years of survey, as well as separate datasets for the comparison of survey techniques and the habitat manipulation experiment (*Figure 7.*1, *Table 7.1*). Forty species plus larvae were recorded overall, totally nearly 11,000 beetles, including 11 ERS specialists and 15 Bembidioniidae. All datasets were dominated by one species, *B. atrocaeruleum*, which is here described as a ‘generalist specialist’ of ERS because of its known distribution across a range of ERS micro-habitats (Bates *et al.* 2006). The resilience of other ERS specialist species in the datasets supported the validity of the study area to investigate environmental change on ERS.

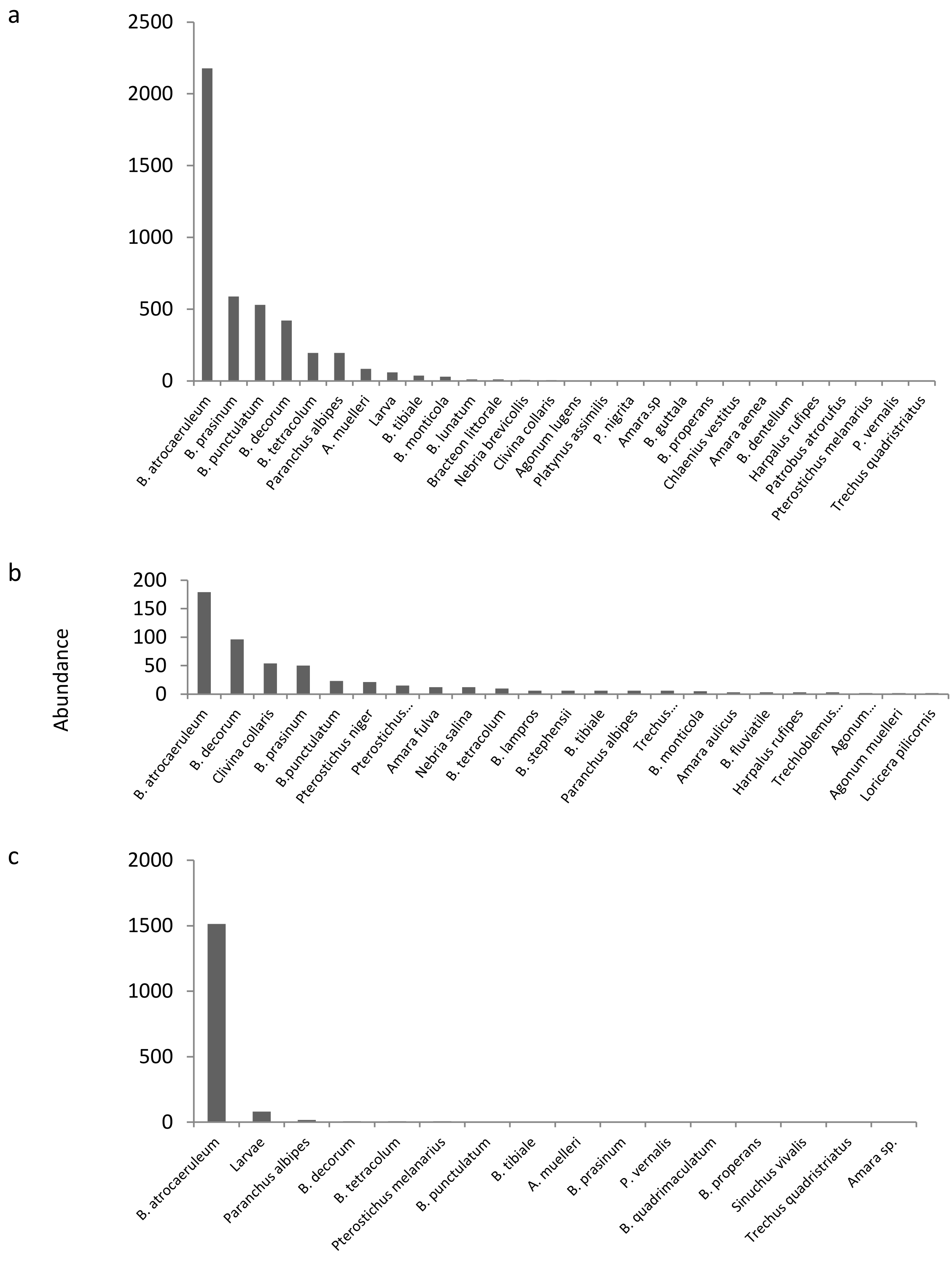


Figure 7.1 Summary of beetles recorded during a) three year study, b) comparative study of sample techniques, and c) experimental habitat manipulation, on ERS in the Usk river system, Wales, between 2008 and 2013.

Table 7.1 40 species of Carabidae plus larvae recorded during several surveys on ERS on the Usk River System, Wales, between 2008 and 2013; see also *Figure 7.1*. **Highlighted species** are ERS specialists (Fowles 2004).

Amara aenea
Amara aulicus
Amara fulva
Amara sp.
Agonum muelleri
Agonum lugens
Agonum marginatum
B. atrocaeruleum
B. decorum
B. dentellum
B.fluviatile
B. guttala
Bembidion lampros
B. lunatum
B. monticola
B. prasinum
B. properans
B. punctulatum
B. quadrimaculatum
Bembidion stephensii
B. tetracolum
B. tibiale
Bracteon littorale
Chlaenius vestitus
Clivina collaris
Harpalus rufipes
Loricera pilicornis
Nebria brevicollis
Nebria salina
Paranchus albipes
Patrobus atrorufus
Platynus assimilis
Pterostichus melanarius
P.niger
P. nigrita
P. vernalis
P. vernalis
Sinuchus vivalis
Trechloblemus micros
Trechus quadristriatus
Larva

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Appendices

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Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2009	1	1a	1	1	2	2	1	1	0.00	1	1	0.00	0	0	0	0	**0**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	1	1b	2	1	2	11	2	2	0.30	11	12	1.08	0	0	0	0	**8**	**3**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	1	1c	3	1	3	26	2	3	0.48	23	35	1.54	0	0	0	0	**16**	**0**	**0**	0	**0**	**0**	**0**	0	**7**	0	**0**	0	**0**	**0**	0	0	3	0	0	0	0	0	0	**0**
2009	1	1d	4	1	5	15	4	5	0.70	9	44	1.64	0	0	0	0	**3**	**3**	**0**	0	**0**	**1**	**0**	0	**0**	0	**2**	0	**0**	**0**	0	0	6	0	0	0	0	0	0	**0**
2009	1	1e	5	1	6	13	4	6	0.78	10	54	1.73	0	0	0	0	**6**	**2**	**0**	0	**0**	**1**	**0**	0	**0**	1	**0**	0	**0**	**1**	0	0	2	0	0	0	0	0	0	**0**
2009	1	1f	6	1	5	23	2	6	0.78	16	70	1.85	0	0	0	0	**12**	**0**	**0**	2	**0**	**0**	**0**	0	**0**	2	**0**	0	**0**	**4**	0	0	3	0	0	0	0	0	0	**0**
2009	1	1a	7	2	3	5	3	7	0.85	5	75	1.88	0	0	0	0	**2**	**0**	**0**	0	**0**	**1**	**2**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	1	1b	8	2	4	18	4	8	0.90	18	93	1.97	0	0	0	0	**10**	**2**	**0**	0	**0**	**0**	**3**	0	**3**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	1	1c	9	2	4	26	2	8	0.90	23	116	2.06	0	0	0	0	**20**	**0**	**0**	0	**0**	**0**	**3**	0	**0**	1	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2009	1	1d	10	2	4	15	4	8	0.90	15	131	2.12	0	0	0	0	**9**	**4**	**0**	0	**0**	**0**	**0**	0	**1**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	1	1e	11	2	2	16	2	8	0.90	16	147	2.17	0	0	0	0	**14**	**2**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	1	1f	12	2	3	48	2	8	0.90	47	194	2.29	0	0	0	0	**45**	**2**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log_{10} cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log_{10} cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2009	1	1a	13	3	1	1	1	8	0.90	1	195	2.29	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	1	1b	14	3	3	16	3	8	0.90	16	211	2.32	0	0	0	0	14	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	1	1c	15	3	4	19	3	8	0.90	17	228	2.36	0	0	0	0	15	1	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	1	1d	16	3	3	4	3	8	0.90	4	232	2.37	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	1	1e	17	3	2	21	2	8	0.90	21	243	2.39	0	0	0	0	20	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	1	1f	18	3	2	41	2	8	0.90	41	284	2.45	0	0	0	0	40	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	2	2a	19	1	6	25	4	9	0.95	15	299	2.48	0	0	0	0	7	6	0	0	0	0	0	0	0	9	1	0	0	0	0	0	1	0	0	0	0	0	0	1
2009	2	2b	20	1	6	14	4	9	0.95	12	311	2.49	0	0	0	0	3	5	0	0	0	0	0	0	3	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
2009	2	2c	21	1	2	6	2	9	0.95	6	317	2.50	0	0	0	0	2	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	2	2d	22	1	3	18	2	9	0.95	17	334	2.52	0	0	0	0	0	2	0	0	0	0	15	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	2	2a	23	2	4	27	4	9	0.95	27	361	2.56	0	0	0	0	10	7	0	0	0	0	6	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009	2	2b	24	2	4	9	4	9	0.95	9	370	2.57	0	0	0	0	3	3	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log_{10} cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log_{10} cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2009	2	2c	25	2	5	12	4	9	0.95	11	381	2.58	0	0	0	0	**3**	**1**	**0**	0	**0**	**0**	**3**	0	**4**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	2	2d	26	2	5	28	5	9	0.95	28	409	2.61	0	0	0	0	**4**	**1**	**0**	0	**0**	**0**	**21**	0	**1**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	2	2a	27	3	5	12	4	9	0.95	10	419	2.62	0	0	0	0	**5**	**1**	**0**	0	**0**	**0**	**3**	0	**0**	0	**1**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2009	2	2b	28	3	1	2	1	9	0.95	2	421	2.62	0	0	0	0	**2**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	2	2c	29	3	3	3	3	9	0.95	3	424	2.63	0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**1**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	2	2d	30	3	1	4	1	9	0.95	4	428	2.63	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**4**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	3	3a	31	1	7	28	5	9	0.95	26	474	2.68	0	0	0	0	**6**	**4**	**0**	0	**0**	**0**	**7**	0	**8**	1	**1**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	3	3b	32	1	4	31	4	9	0.95	31	505	2.70	0	0	0	0	**19**	**8**	**0**	0	**0**	**2**	**0**	0	**2**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	3	3a	33	2	2	6	2	9	0.95	6	511	2.71	0	0	0	0	**5**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	3	3b	34	2	3	11	3	9	0.95	11	522	2.72	0	0	0	0	**7**	**3**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	3	3a	35	3	3	4	3	9	0.95	4	526	2.72	0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**2**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	3	3b	36	3	0	0	0	9	0.95	0	526	2.72	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**

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2009	4	4a	37	1	2	6	1	9	0.95	4	530	2.72	0	0	0	0	**0**	**4**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2009	4	4b	38	1	6	15	3	10	1.00	12	542	2.73	0	0	0	1	**5**	**0**	**1**	0	**0**	**0**	**0**	0	**6**	1	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	4	4a	39	2	3	5	2	10	1.00	4	546	2.74	0	0	0	0	**3**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	4	4b	40	2	3	18	1	10	1.00	3	549	2.74	0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	14	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	4	4a	41	3	1	2	1	10	1.00	2	551	2.74	0	0	0	0	**2**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	4	4b	42	3	0	0	0	10	1.00	0	551	2.74	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5c	43	1	3	14	3	10	1.00	14	565	2.75	0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**8**	0	**3**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5d	44	1	1	4	1	10	1.00	4	569	2.76	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**4**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5e	45	1	3	5	3	10	1.00	5	574	2.76	0	0	0	0	**3**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5f	46	1	4	17	3	10	1.00	16	590	2.77	0	0	0	0	**9**	**0**	**0**	0	**0**	**0**	**0**	0	**4**	0	**3**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	5	5c	47	2	4	38	4	10	1.00	38	628	2.80	0	0	0	0	**30**	**3**	**0**	0	**0**	**0**	**0**	0	**4**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5d	48	2	3	12	2	10	1.00	11	639	2.81	0	0	0	0	**2**	**0**	**0**	0	**0**	**0**	**0**	0	**9**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2009	5	5e	49	2	3	15	2	10	1.00	14	653	2.81	0	0	0	0	**10**	**4**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5f	50	2	5	23	5	10	1.00	23	676	2.83	0	0	0	0	**17**	**1**	**0**	0	**0**	**0**	**1**	0	**2**	0	**2**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5c	51	3	1	3	1	10	1.00	3	679	2.83	0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5d	52	3	1	1	1	10	1.00	1	682	2.83	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5e	53	3	3	9	3	10	1.00	9	691	2.84	0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**5**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	5	5f	54	3	2	2	2	10	1.00	2	693	2.84	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**1**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6a	55	1	2	24	1	10	1.00	23	716	2.85	0	0	0	0	**23**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	6	6b	56	1	3	48	2	10	1.00	47	763	2.88	0	0	0	0	**46**	**0**	**0**	0	**0**	**1**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6c	57	1	5	47	3	10	1.00	44	807	2.91	0	0	0	0	**40**	**0**	**0**	0	**0**	**1**	**0**	0	**3**	1	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2009	6	6d	58	1	4	52	3	10	1.00	42	849	2.93	0	0	0	0	**33**	**0**	**0**	0	**0**	**6**	**0**	0	**3**	0	**0**	10	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6e	59	1	7	40	5	10	1.00	34	883	2.95	0	0	0	0	**8**	**1**	**0**	0	**0**	**0**	**1**	0	**23**	4	**1**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2009	6	6f	60	1	6	47	4	10	1.00	44	927	2.97	0	0	0	0	**40**	**0**	**0**	0	**0**	**1**	**1**	0	**2**	1	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2009	6	6g	61	1	4	30	4	10	1.00	30	957	2.98	0	0	0	0	**14**	**1**	**0**	0	**0**	**2**	**0**	0	**13**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6a	62	2	2	23	2	10	1.00	23	980	2.99	0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**22**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6b	63	2	5	22	4	10	1.00	21	1001	3.00	0	0	0	0	**18**	**1**	**0**	0	**0**	**0**	**1**	0	**0**	0	**1**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	6	6c	64	2	7	42	4	10	1.00	39	1040	3.02	0	0	0	0	**35**	**1**	**0**	0	**0**	**1**	**0**	0	**0**	1	**2**	0	**0**	**0**	0	0	0	0	1	1	0	0	0	**0**
2009	6	6d	65	2	5	44	4	10	1.00	43	1083	3.03	0	0	0	0	**40**	**1**	**0**	0	**0**	**1**	**0**	0	**0**	0	**1**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	6	6e	66	2	4	4	2	10	1.00	2	1085	3.04	0	0	0	0	**1**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	6	6f	67	2	4	35	4	10	1.00	35	1120	3.05	0	0	0	0	**30**	**3**	**0**	0	**0**	**0**	**0**	0	**1**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6g	68	2	3	18	3	10	1.00	18	1138	3.06	0	0	0	0	**14**	**0**	**0**	0	**0**	**0**	**0**	0	**3**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6a	69	3	1	14	1	10	1.00	14	1152	3.06	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**14**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6b	70	3	2	17	2	10	1.00	17	1169	3.07	0	0	0	0	**13**	**0**	**0**	0	**0**	**0**	**4**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6c	71	3	2	48	2	10	1.00	48	1217	3.09	0	0	0	0	**46**	**0**	**0**	0	**0**	**2**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6d	72	3	2	83	1	10	1.00	82	1299	3.11	0	0	0	0	**82**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2009	6	6e	73	3	3	3	2	10	1.00	2	1301	3.11	0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2009	6	6f	74	3	3	5	2	10	1.00	4	1305	3.12	0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**3**	0	**1**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2009	6	6g	75	3	4	16	4	10	1.00	16	1321	3.12	0	0	0	0	**1**	**3**	**0**	0	**0**	**0**	**10**	0	**2**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1a		1	5	10				9			0	0	0	0	**5**	**2**	**0**	0	**0**	**0**	**1**	0	**0**	0	**0**	0	**0**	**0**	0	1	0	0	0	0	0	0	0	**1**
2010	1	1b		1	4	36				36			0	0	0	0	**3**	**5**	**0**	0	**0**	**0**	**27**	0	**0**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1c		1	5	32				30			0	0	0	0	**24**	**3**	**0**	0	**0**	**0**	**0**	0	**1**	2	**2**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1d		1	5	18				13			0	0	0	4	**6**	**3**	**0**	0	**0**	**0**	**0**	0	**4**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	1	1e		1	4	43				40			0	0	0	1	**35**	**5**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2010	1	1f		1	4	54				48			0	0	0	0	**42**	**6**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	1	5	0	0	0	0	0	0	**0**
2010	1	1a		2	5	13				10			0	0	0	2	**1**	**8**	**0**	0	**0**	**0**	**0**	0	**0**	0	**1**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	1	1b		2	3	13				12			0	0	0	1	**0**	**10**	**0**	0	**0**	**0**	**2**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1c		2	8	46				42			0	0	0	0	**7**	**28**	**0**	0	**0**	**2**	**0**	0	**1**	3	**2**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**2**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log_{10} cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log_{10} cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2010	1	1d		2	4	21				20			0	0	0	1	**16**	**0**	**0**	0	**0**	**0**	**0**	0	**3**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1e		2	3	27				26			0	0	0	0	**21**	**5**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1f		2	6	12				8			0	0	0	1	**2**	**5**	**0**	0	**0**	**0**	**0**	0	**1**	2	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	1	1a		3	1	1				1			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**1**
2010	1	1b		3	1	4				4			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**4**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1c		3	2	21				21			0	0	0	0	**15**	**6**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1d		3	2	2				1			0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	1	1e		3	1	1				1			0	0	0	0	**0**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	1	1f		3	3	17				16			0	0	0	0	**12**	**4**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	2	2a		1	6	20				16			0	0	0	0	**4**	**0**	**0**	0	**0**	**0**	**1**	0	**10**	2	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**1**
2010	2	2b		1	4	7				7			0	0	0	0	**1**	**1**	**0**	0	**0**	**0**	**1**	0	**4**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	2	2c		1	3	10				10			0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**4**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**3**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2010	2	2d		1	3	10				10			0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**2**	0	**5**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	2	2a		2	8	70				65			0	0	1	0	**45**	**17**	**0**	0	**0**	**0**	**1**	0	**1**	3	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**1**
2010	2	2b		2	7	18				12			0	0	0	3	**3**	**1**	**0**	0	**0**	**1**	**1**	0	**6**	3	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	2	2c		2	5	16				9			0	0	0	2	**2**	**5**	**0**	0	**0**	**0**	**2**	0	**0**	5	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	2	2d		2	5	47				22			0	0	0	0	**16**	**1**	**0**	0	**0**	**2**	**0**	0	**3**	25	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	2	2a		3	2	2				1			1	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**1**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	2	2b		3	1	1				1			0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	2	2c		3	2	2				1			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	2	2d		3	3	15				14			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**13**	0	**1**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	3	3a		1	4	12				8			0	0	0	3	**7**	**0**	**0**	0	**0**	**0**	**1**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	3	3b		1	3	26				26			0	0	0	0	**11**	**2**	**0**	0	**0**	**0**	**0**	0	**13**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	3	3a		2	3	4				4			0	0	0	0	**1**	**2**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2010	3	3b		2	5	25				22			0	0	0	3	**12**	**3**	**0**	0	**0**	**1**	**0**	0	**6**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	3	3a		3	1	2				2			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**2**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	3	3b		3	3	6				6			0	0	0	0	**1**	**4**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	4	4a		1	2	11				3			0	0	0	0	**0**	**3**	**0**	0	**0**	**0**	**0**	0	**0**	8	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	4	4b		1	4	18				12			0	0	0	0	**11**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	5	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	4	4a		2	6	23				21			0	0	0	1	**12**	**5**	**0**	0	**0**	**0**	**0**	0	**2**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	1	0	0	**2**
2010	4	4b		2	7	29				16			0	0	0	3	**11**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	4	**4**	0	**0**	**0**	1	0	5	0	0	0	0	0	0	**1**
2010	4	4a		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	4	4b		3	2	2				2			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**1**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	5	5a		1	6	15				8			0	0	0	1	**3**	**0**	**0**	0	**0**	**0**	**4**	0	**1**	4	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2010	5	5b		1	6	21				17			0	0	0	1	**9**	**2**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**6**
2010	5	5c		1	7	19				15			0	0	0	1	**2**	**1**	**0**	0	**0**	**0**	**0**	0	**11**	1	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**1**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2010	5	5d		1	5	18				13			0	0	0	2	10	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0
2010	5	5e		1	3	15				13			0	0	0	0	7	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
2010	5	5f		1	5	14				8			0	0	0	3	0	0	0	0	0	0	6	0	2	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0
2010	5	5a		2	6	17				12			0	0	0	1	3	2	0	0	0	0	2	0	5	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
2010	5	5b		2	3	17				15			0	0	0	2	14	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	5	5c		2	5	16				14			0	0	0	2	3	1	0	0	0	0	0	0	9	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	5	5d		2	3	6				3			0	0	0	3	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	5	5e		2	2	5				4			0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
2010	5	5f		2	1	5				5			0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	5	5a		3	0	0				0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	5	5b		3	0	0				0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	5	5c		3	0	0				0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2010	5	5d		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	5	5e		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	5	5f		3	1	7				7			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**7**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	6	6a		1	4	6				3			0	0	0	0	**1**	**1**	**0**	0	**0**	**0**	**1**	0	**0**	0	**0**	0	**0**	**0**	0	0	3	0	0	0	0	0	0	**0**
2010	6	6b		1	1	2				2			0	0	0	0	**2**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	6	6c		1	3	14				13			0	0	0	0	**12**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2010	6	6d		1	2	6				5			0	1	0	0	**5**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2010	6	6e		1	7	24				6			0	1	0	2	**5**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	4	**0**	0	**0**	**0**	0	0	10	0	1	0	0	0	0	**0**
2010	6	6f		1	1	4				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	4	0	0	0	0	0	0	**0**
2010	6	6g		1	6	15				10			0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**4**	0	**5**	1	**0**	0	**0**	**0**	0	0	4	0	0	0	0	0	0	**0**
2010	6	6a		2	8	17				15			0	0	1	0	**3**	**4**	**0**	0	**4**	**0**	**2**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	1	0	0	**1**
2010	6	6b		2	4	38				35			0	0	0	0	**29**	**3**	**0**	0	**3**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	3	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2010	6	6c		2	4	19				8			0	0	0	0	7	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	10	0	0	0	0	0	0	0
2010	6	6d		2	6	54				52			0	0	0	0	2	1	0	0	1	0	20	0	28	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
2010	6	6e		2	6	20				14			0	0	0	0	10	1	0	0	1	0	0	0	2	1	0	0	0	0	0	0	5	0	0	0	0	0	0	0
2010	6	6f		2	3	9				3			0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	0
2010	6	6g		2	4	6				6			0	0	0	0	0	1	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2010	6	6a		3	1	6				6			0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	6	6b		3	0	0				0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	6	6c		3	1	32				32			0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	6	6d		3	1	19				19			0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	6	6e		3	4	18				16			0	0	0	0	11	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
2010	6	6f		3	1	2				2			0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2010	6	6g		3	4	8				8			0	0	0	0	1	0	0	0	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

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Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2011	1	1a		1	4	8				4			0	0	0	3	**0**	**2**	**0**	0	**0**	**0**	**2**	1	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1b		1	3	13				13			0	0	0	0	**0**	**1**	**0**	0	**0**	**0**	**11**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**1**
2011	1	1c		1	6	22				15			0	0	0	1	**5**	**9**	**0**	0	**0**	**0**	**0**	0	**0**	3	**0**	0	**0**	**0**	0	0	3	0	0	0	0	0	0	**1**
2011	1	1d		1	5	14				1			0	0	1	1	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	4	**0**	0	**0**	**0**	0	0	7	0	0	0	0	0	0	**1**
2011	1	1e		1	6	18				9			0	0	0	1	**6**	**2**	**0**	0	**0**	**0**	**1**	0	**0**	1	**0**	0	**0**	**0**	0	0	7	0	0	0	0	0	0	**0**
2011	1	1f		1	4	29				15			0	0	0	0	**13**	**2**	**0**	0	**0**	**0**	**0**	0	**0**	11	**0**	0	**0**	**0**	0	0	3	0	0	0	0	0	0	**0**
2011	1	1a		2	4	46				46			0	0	0	0	**34**	**9**	**0**	0	**0**	**1**	**2**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1b		2	5	81				80			0	0	0	0	**9**	**10**	**0**	0	**0**	**0**	**57**	0	**4**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	1	1c		2	4	92				90			0	0	0	0	**70**	**20**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	1	0	0	**0**
2011	1	1d		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1e		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1f		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**

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Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2011	1	1a		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1b		3	2	20				20			0	0	0	0	**0**	**8**	**0**	0	**0**	**0**	**12**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1c		3	3	24				24			0	0	0	0	**1**	**20**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**3**
2011	1	1d		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1e		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	1	1f		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	2	2a		1	4	23				18			0	0	0	0	**0**	**9**	**0**	0	**0**	**0**	**1**	0	**8**	5	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	2	2b		1	5	30				22			0	0	0	0	**9**	**3**	**0**	0	**0**	**0**	**0**	0	**10**	7	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	2	2c		1	7	36				29			0	0	0	3	**3**	**1**	**0**	0	**0**	**0**	**18**	0	**7**	1	**0**	0	**0**	**0**	0	0	3	0	0	0	0	0	0	**0**
2011	2	2d		1	4	21				15			0	0	0	0	**0**	**2**	**0**	0	**0**	**0**	**9**	0	**4**	0	**0**	0	**0**	**0**	0	0	6	0	0	0	0	0	0	**0**
2011	2	2a		2	5	22				11			0	0	0	0	**3**	**6**	**0**	0	**0**	**0**	**0**	0	**2**	9	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2011	2	2b		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2011	2	2c		2	2	24				24			0	0	0	0	0	0	0	0	0	0	22	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	2	2d		2	2	55				55			0	0	0	0	0	0	0	0	0	0	51	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	2	2a		3	2	10				9			0	0	0	0	0	9	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	2	2b		3	4	4				3			0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2011	2	2c		3	2	3				3			0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2011	2	2d		3	3	31				30			0	0	0	1	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
2011	3	3a		1	3	15				9			0	0	0	6	0	0	0	0	0	0	7	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	3	3b		1	5	25				23			0	0	0	2	8	2	0	0	0	0	1	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	3	3a		2	6	37				31			0	0	0	5	8	3	0	0	0	0	16	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	3	3b		2	0	0				0			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	3	3a		3	2	20				20			0	0	0	0	0	0	0	0	0	0	18	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2011	3	3b		3	1	1				0			0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2011	4	4a		1	4	9				7			0	0	0	1	**0**	**4**	**0**	0	**0**	**0**	**0**	0	**3**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	4	4b		1	3	16				13			0	0	0	0	**13**	**0**	**0**	0	**0**	**0**	**0**	1	**0**	2	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	4	4a		2	4	23				21			0	0	0	0	**12**	**6**	**0**	0	**0**	**0**	**0**	0	**3**	2	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	4	4b		2	4	27				25			0	0	0	0	**23**	**2**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	4	4a		3	1	20				20			0	0	0	0	**0**	**20**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	4	4b		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5a		1	7	26				16			0	0	0	0	**2**	**1**	**0**	0	**0**	**0**	**0**	0	**11**	6	**0**	0	**0**	**0**	0	2	2	0	0	0	0	0	0	**2**
2011	5	5b		1	2	5				5			0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**0**	0	**2**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5c		1	3	12				9			0	0	0	1	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**9**	2	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5d		1	5	12				10			0	0	0	1	**2**	**2**	**0**	0	**0**	**0**	**0**	0	**6**	0	**0**	0	**0**	**0**	0	1	0	0	0	0	0	0	0	**0**
2011	5	5e		1	3	9				8			0	0	0	0	**3**	**0**	**0**	0	**0**	**0**	**0**	0	**5**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5f		1	5	30				25			0	0	0	2	**0**	**0**	**0**	0	**0**	**0**	**2**	0	**23**	1	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2011	5	5a		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5b		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5c		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5d		2	5	40				39			0	0	0	0	**14**	**1**	**0**	0	**0**	**0**	**6**	0	**18**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5e		2	3	42				42			0	0	0	0	**13**	**0**	**0**	0	**0**	**0**	**14**	0	**15**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5f		2	5	46				43			0	0	0	1	**0**	**0**	**0**	0	**0**	**0**	**26**	0	**17**	1	**0**	0	**0**	**0**	0	0	0	1	0	0	0	0	0	**0**
2011	5	5a		3	7	22				17			0	0	0	2	**0**	**0**	**0**	0	**0**	**0**	**3**	0	**7**	0	**0**	0	**1**	**0**	0	0	2	0	1	0	0	0	0	**6**
2011	5	5b		3	7	12				10			0	0	0	1	**2**	**3**	**0**	0	**0**	**0**	**0**	0	**1**	1	**0**	0	**1**	**0**	0	0	0	0	0	0	0	0	0	**3**
2011	5	5c		3	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5d		3	5	13				12			0	0	0	1	**0**	**3**	**0**	0	**0**	**0**	**2**	0	**6**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**1**
2011	5	5e		3	1	1				1			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	5	5f		3	2	11				11			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**2**	0	**9**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.

Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2011	6	6a		1	3	4				2			0	0	1	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**2**
2011	6	6b		1	5	15				14			0	0	0	0	**11**	**0**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**1**	0	1	0	0	0	0	0	0	0	**1**
2011	6	6c		1	6	22				14			0	0	0	0	**8**	**1**	**0**	0	**0**	**0**	**0**	0	**4**	0	**0**	0	**0**	**0**	0	1	7	0	0	0	0	0	0	**1**
2011	6	6d		1	5	19				11			0	0	0	0	**5**	**0**	**0**	0	**0**	**0**	**0**	0	**5**	1	**0**	0	**0**	**0**	0	0	7	0	0	0	0	0	0	**1**
2011	6	6e		1	7	24				13			0	0	0	0	**4**	**1**	**0**	0	**0**	**0**	**0**	0	**2**	2	**0**	0	**0**	**0**	0	0	8	0	0	0	0	0	1	**6**
2011	6	6f		1	4	6				3			0	0	0	0	**1**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	3	0	0	0	0	0	0	**1**
2011	6	6g		1	4	9				2			0	0	0	5	**0**	**1**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2011	6	6a		2	5	64				64			0	0	0	0	**60**	**1**	**0**	0	**0**	**0**	**1**	0	**1**	0	**1**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	6	6b		2	4	94				93			0	0	0	0	**91**	**1**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	6	6c		2	3	85				84			0	0	0	0	**83**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	6	6d		2	4	67				66			0	0	0	0	**62**	**1**	**0**	0	**0**	**0**	**0**	0	**3**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	6	6e		2	0	0				0			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**

Appendix 1: Beetle dataset for three years of timed hand searches, completing three sample visits to 6 sites each year, 2009 to 2011.																																								
Year	Site	Sample location	Sample No.	Sample Visit 1-3	Species richness	Beetle abundance	ERS specialist spp richness	Cumulative ERS specialist spp richness 2009	Log$_{10}$ cumulative ERS spp richness 2009	ERS specialist beetle abundance	Cumulative ERS specialist beetle abundance 2009	Log$_{10}$ cumulative ERS specialist beetle abundance	*Amara aenea*	*Amara.sp*	*Agonum lugens*	*A. muelleri*	***B. atrocaeruleum***	***B. decorum***	***B. dentellum***	*B. guttala*	***B. lunatum***	***B. monticola***	***B. prasinum***	*B. properans*	***B. punctulatum***	*B. tetracolum*	***B. tibiale***	*Bracteon littorale*	***Chlaenius vestitus***	***Clivina collaris***	*Harpalus rufipes*	*Nebria brevicollis*	*Paranchus albipes*	*Patrobus atrorufus*	*Platynus assimilis*	*Pterostichus melanarius*	*P. nigrita*	*P. vernalis*	*Trechus quadristriatus*	**Larva**
2011	6	6f		2	3	50				48			0	0	0	0	**47**	**0**	**0**	0	**0**	**0**	**1**	0	**0**	2	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	6	6g		2	5	61				59			0	0	0	0	**28**	**0**	**0**	0	**0**	**0**	**3**	0	**28**	1	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	6	6a		3	2	5				5			0	0	0	0	**4**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**1**
2011	6	6b		3	2	25				24			0	0	0	0	**24**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	1	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	6	6c		3	3	68				66			0	0	0	0	**65**	**1**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	2	0	0	0	0	0	0	**0**
2011	6	6d		3	4	7				6			0	0	0	0	**4**	**1**	**0**	0	**0**	**0**	**0**	0	**1**	0	**0**	0	**0**	**0**	0	0	1	0	0	0	0	0	0	**0**
2011	6	6e		3	1	5				5			0	0	0	0	**0**	**0**	**0**	0	**0**	**0**	**0**	0	**5**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	6	6f		3	1	1				1			0	0	0	0	**1**	**0**	**0**	0	**0**	**0**	**0**	0	**0**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**0**
2011	6	6g		3	4	10				10			0	0	0	0	**3**	**3**	**0**	0	**0**	**0**	**0**	0	**3**	0	**0**	0	**0**	**0**	0	0	0	0	0	0	0	0	0	**1**

Appendix 2 Habitat variables recorded on each site, each year.[1]

Year	Site	Bare	Cover	Scrub	Canopy	Flat	Gentle	Steep	Simple	Humped	Complex	Shore length	Width	Area	Heterogeneity	Fractal dimension
2009	1	100	0	0	0	90	0	10	90	10	0	284	30	7952	5	-
2009	1	75	15	10	0	90	5	5	90	10	0	284	15	7952	5	-
2009	1	95	5	0	0	20	60	20	60	20	20	284	16	7952	5	-
2009	1	80	15	5	0	50	30	20	70	20	10	284	30	7952	5	-
2009	1	95	2.5	2.5	0	90	5	5	95	5	0	284	23	7952	5	-
2009	1	85	15	0	0	80	0	20	80	20	0	284	30	7952	5	-
2009	2	60	20	20	0	100	0	0	90	10	0	250	14	12250	3	-
2009	2	60	40	0	0	100	0	0	90	10	0	250	22	12250	3	-
2009	2	30	70	0	0	100	0	0	90	10	0	250	60	12250	3	-
2009	2	40	60	0	0	100	0	0	90	10	0	250	100	12250	3	-
2009	3	100	0	0	0	95	5	0	95	5	0	98	4	1176	3	-
2009	3	80	20	0	0	20	70	10	90	10	0	98	19	1176	3	-
2009	4	95	5	0	0	0	95	5	95	5	0	86	5	645	2	-
2009	4	95	5	0	0	0	95	5	95	5	0	86	10	645	2	-
2009	5	50	50	0	0	0	100	0	100	0	0	193	16	5211	2	-
2009	5	80	20	0	0	0	100	0	40	60	0	193	18	5211	2	-
2009	5	70	30	0	0	90	5	5	95	5	0	193	30	5211	2	-
2009	5	95	5	0	0	100	0	0	100	0	0	193	42	5211	2	-
2009	6	99	1	0	0	100	0	0	100	0	0	340	38	6120	5	-
2009	6	95	5	0	0	70	20	10	80	20	0	340	35	6120	5	-
2009	6	70	10	20	0	0	60	40	20	80	0	340	22	6120	5	-
2009	6	100	0	0	0	0	60	40	80	20	0	340	6	6120	5	-
2009	6	100	0	0	0	0	50	50	80	20	0	340	2	6120	5	-
2009	6	75	5	20	0	0	100	0	100	0	0	340	12	6120	5	-
2009	6	75	5	20	0	90	5	5	95	5	0	340	9	6120	5	-
2010	1	90	10	0	0	90	0	10	90	10	0	290	40	13195	5	-
2010	1	50	40	10	0	90	5	5	90	10	0	290	72	13195	5	-
2010	1	50	40	10	0	20	60	20	60	20	20	290	70	13195	5	-
2010	1	30	40	30	0	50	30	20	70	20	10	290	35	13195	5	-
2010	1	80	15	5	0	90	5	5	95	5	0	290	26	13195	5	-
2010	1	80	15	5	0	80	0	20	80	20	0	290	30	13195	5	-
2010	2	60	30	10	0	100	0	0	90	10	0	190	5	7362.5	3	-
2010	2	60	35	5	0	100	0	0	90	10	0	190	20	7362.5	3	-
2010	2	60	35	5	0	100	0	0	90	10	0	190	50	7362.5	3	-
2010	2	70	20	10	0	100	0	0	90	10	0	190	80	7362.5	3	-
2010	3	70	30	0	0	95	5	0	95	5	0	98	17	1421	3	-
2010	3	95	5	0	0	20	70	10	90	10	0	98	12	1421	3	-
2010	4	90	10	0	0	0	95	5	95	5	0	115	6	1035	2	-
2010	4	95	5	0	0	0	95	5	95	5	0	115	12	1035	2	-
2010	5	95	5	5	0	80	10	10	90	10	0	280	20	6664	3	-
2010	5	50	50	0	0	0	100	0	100	0	0	280	50	6664	3	-
2010	5	60	40	0	0	0	100	0	100	0	0	280	35	6664	3	-
2010	5	40	60	0	0	0	100	0	40	60	0	280	16	6664	3	-
2010	5	70	30	0	0	90	5	5	95	5	0	280	19	6664	3	-
2010	5	100	0	0	0	100	0	0	100	0	0	280	3	6664	3	-
2010	6	100	0	0	0	100	0	0	100	0	0	370	40	7907	5	-
2010	6	100	0	0	0	20	10	80	80	20	0	370	32	7907	5	-

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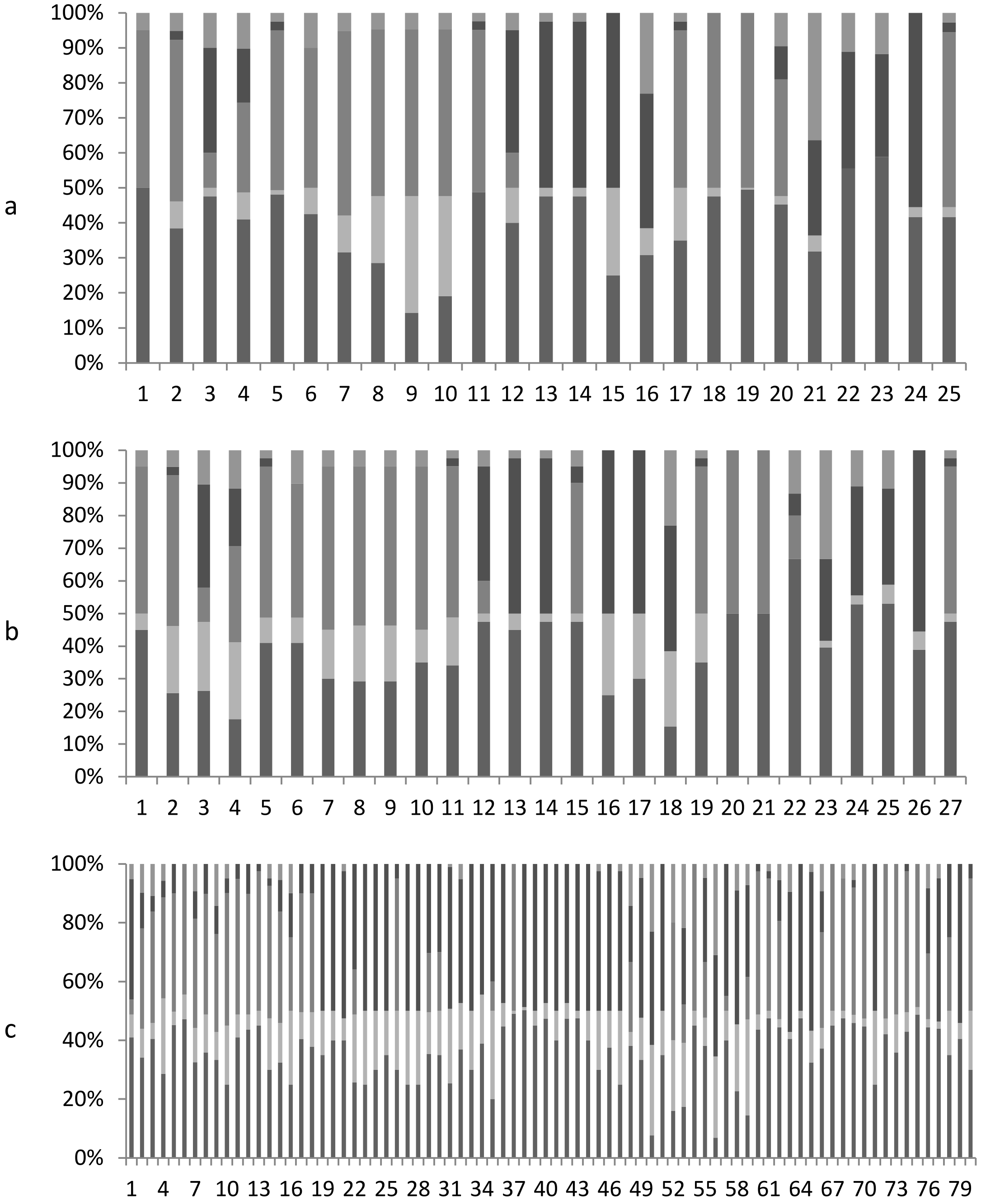
[1] Each site varied in the number of sample locations available at 50 m intervals, e.g., Site 1 = six locations, Site 2 = four locations etc, with habitat variables recorded at each location (see Section 2.2 for further explanation). Variables from bare through to complex were recorded on a percentage cover basis, site dimensions were recorded in m and m^2, heterogeneity was based upon a category (*Table 4.1* main text) and fractal dimension (2011 only) was generated through processing of sediment photographs in Image J (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2012). Habitat variables were recorded once each year (during first of three sample visits) during 2009 and 2010 and three times (during each sample visit) in 2011.

Appendix 2 Habitat variables recorded on each site, each year.[1]

Year	Site	Bare	Cover	Scrub	Canopy	Flat	Gentle	Steep	Simple	Humped	Complex	Shore length	Width	Area	Heterogeneity	Fractal dimension
2010	6	95	5	0	0	0	60	40	20	80	0	370	30	7907	5	-
2010	6	95	5	0	0	0	60	40	80	20	0	370	11	7907	5	-
2010	6	90	10	0	0	0	50	50	80	20	0	370	4	7907	5	-
2010	6	70	10	5	5	0	100	0	100	0	0	370	25	7907	5	-
2010	6	95	5	0	0	90	5	5	95	5	0	370	10	7907	5	-
2011	1	80	15	5	0	10	80	10	90	10	0	304	30	12160	5	1.69
2011	1	70	20	10	0	70	25	5	80	20	0	304	70	12160	5	1.83
2011	1	75	10	5	10	70	10	20	60	20	20	304	62	12160	5	1.8
2011	1	50	45	5	0	60	10	30	90	10	0	304	32	12160	5	1.79
2011	1	90	9	1	0	80	20	0	100	0	0	304	24	12160	5	1.76
2011	1	85	15	0	0	80	0	20	80	0	20	304	24	12160	5	1.79
2011	1	70	25	5	0	80	20	0	80	20	0	333	45	12321	5	1.69
2011	1	70	25	5	0	80	20	0	100	0	0	333	63	12321	5	1.83
2011	1	70	20	5	5	70	20	10	70	30	0	333	45	12321	5	1.8
2011	1	50	40	5	5	90	10	0	90	10	0	333	22	12321	5	1.79
2011	1	80	15	5	0	90	10	0	100	0	0	333	23	12321	5	1.76
2011	1	85	10	5	0	80	20	0	100	0	0	333	24	12321	5	1.79
2011	1	90	10	0	0	95	5	0	100	0	0	330	45	14520	5	1.69
2011	1	60	35	5	0	90	5	5	90	10	0	330	75	14520	5	1.83
2011	1	60	25	10	5	70	20	10	80	10	10	330	70	14520	5	1.8
2011	1	50	50	0	0	50	30	20	80	20	0	330	24	14520	5	1.79
2011	1	80	18	2	0	80	20	0	100	0	0	330	25	14520	5	1.76
2011	1	75	23	2	0	80	20	0	100	0	0	330	24	14520	5	1.79
2011	2	70	30	0	0	0	100	0	100	0	0	203	4	5126	3	1.7
2011	2	80	20	0	0	0	100	0	100	0	0	203	12	5126	3	1.74
2011	2	80	15	5	0	0	100	0	95	5	0	203	24	5126	3	1.69
2011	2	50	45	5	0	30	70	0	100	0	0	203	61	5126	3	1.71
2011	2	50	50	0	0	0	100	0	100	0	0	196	5	3920	3	1.7
2011	2	60	40	0	0	0	100	0	100	0	0	196	13	3920	3	1.74
2011	2	70	30	0	0	0	100	0	100	0	0	196	18	3920	3	1.69
2011	2	60	40	0	0	90	10	0	100	0	0	196	44	3920	3	1.71
2011	2	50	50	0	0	0	100	0	100	0	0	200	5	3700	3	1.7
2011	2	50	50	0	0	0	100	0	100	0	0	200	10	3700	3	1.74
2011	2	70	28	2	0	40	60	0	100	0	0	200	19	3700	3	1.69
2011	2	70	30	0	0	40	60	0	100	0	0	200	40	3700	3	1.71
2011	3	50	50	0	0	0	95	5	98	2	0	100	16	1700	3	1.76
2011	3	70	30	0	0	0	80	20	90	10	0	100	18	1700	3	1.68
2011	3	60	40	0	0	0	100	0	100	0	0	96	15	1584	3	1.76
2011	3	70	30	0	0	0	80	20	100	0	0	96	18	1584	3	1.68
2011	3	40	60	0	0	20	80	0	80	0	20	100	15	1800	3	1.76
2011	3	85	15	0	0	0	90	10	100	0	0	100	21	1800	3	1.68
2011	4	98	2	0	0	100	0	0	100	0	0	84	6	756	2	1.68
2011	4	98	2	0	0	0	95	5	100	0	0	84	12	756	2	1.91
2011	4	90	10	0	0	0	100	0	100	0	0	88	5	748	2	1.68
2011	4	90	10	0	0	0	90	10	100	0	0	88	12	748	2	1.91
2011	4	80	20	0	0	0	100	0	100	0	0	88	6	792	2	1.68
2011	4	90	10	0	0	0	90	100	100	0	0	88	12	792	2	1.91
2011	5	95	5	0	0	0	100	0	100	0	0	300	3	4851	3	1.74
2011	5	80	20	0	0	0	100	0	100	0	0	300	18	4851	3	1.66
2011	5	60	40	0	0	0	95	5	95	5	0	300	14	4851	3	1.72
2011	5	75	25	0	0	0	100	0	100	0	0	300	18	4851	3	1.77
2011	5	50	50	0	0	0	95	5	95	5	0	300	28	4851	3	1.74
2011	5	80	10	5	5	50	40	10	70	30	0	300	16	4851	3	1.74
2011	5	70	30	0	0	0	100	0	85	10	5	266	16	4256	3	1.66

Appendix 2 Habitat variables recorded on each site, each year.[1]

Year	Site	Bare	Cover	Scrub	Canopy	Flat	Gentle	Steep	Simple	Humped	Complex	Shore length	Width	Area	Heterogeneity	Fractal dimension
2011	5	20	80	0	0	0	100	0	40	60	0	266	16	4256	3	1.72
2011	5	70	30	0	0	0	100	0	100	0	0	266	12	4256	3	1.77
2011	5	40	60	0	0	100	0	0	50	50	0	266	26	4256	3	1.74
2011	5	40	50	0	10	30	60	10	40	50	10	266	10	4256	3	1.74
2011	5	90	10	0	0	100	0	0	100	0	0	318	3	4770	3	1.74
2011	5	80	20	0	0	40	60	0	90	10	0	318	17	4770	3	1.66
2011	5	20	80	0	0	0	100	0	10	90	0	318	14	4770	3	1.72
2011	5	80	20	0	0	10	90	0	100	0	0	318	16	4770	3	1.77
2011	5	50	50	0	0	0	100	0	80	20	0	318	26	4770	3	1.74
2011	5	30	68	0	2	30	65	5	80	15	5	318	14	4770	3	1.74
2011	6	85	10	0	5	95	5	0	100	0	0	379	51	8501	5	1.82
2011	6	95	5	0	0	90	5	5	95	5	0	379	34	8501	5	1.76
2011	6	80	5	10	5	60	25	15	85	10	5	379	27	8501	5	1.72
2011	6	85	5	5	5	0	100	0	80	20	0	379	14	8501	5	1.74
2011	6	95	5	0	0	0	100	0	100	0	0	379	7	8501	5	1.74
2011	6	60	20	10	10	0	100	0	95	5	0	379	10	8501	5	1.71
2011	6	80	15	2.5	2.5	70	30	0	80	20	0	379	14	8501	5	1.76
2011	6	90	10	0	0	100	0	0	100	0	0	378	57	8316	5	1.82
2011	6	95	5	0	0	90	0	10	10	10	0	378	34	8316	5	1.76
2011	6	85	5	5	5	80	5	15	85	10	5	378	27	8316	5	1.72
2011	6	85	5	5	5	100	0	0	100	0	0	378	12	8316	5	1.74
2011	6	50	50	0	0	0	100	0	100	0	0	378	5	8316	5	1.74
2011	6	80	10	0	10	100	0	0	100	0	0	378	10	8316	5	1.71
2011	6	70	25	0	5	100	0	0	100	0	0	378	10	8316	5	1.76
2011	6	85	13	0	2	95	5	0	100	0	0	378	56	8316	5	1.82
2011	6	95	5	0	0	95	0	5	100	0	0	378	32	8316	5	1.76
2011	6	80	5	10	5	40	40	20	80	15	5	378	26	8316	5	1.72
2011	6	90	5	0	5	0	100	0	90	10	0	378	12	8316	5	1.74
2011	6	70	30	0	0	50	50	0	100	0	0	378	5	8316	5	1.74
2011	6	75	10	5	10	0	100	0	100	0	0	378	12	8316	5	1.71
2011	6	60	40	0	0	90	10	0	100	0	0	378	11	8316	5	1.76



Appendix 3 Proportional distribution of five coverage-based habitat variables identified through principal components analysis (■Bare, ■ Ground Cover, ■ Flat, ■ Gentle, ■ Humped) throughout the study area during three years. Numbers refer to sample locations: a) 25 sample locations in 2009 (1-6 Site 1, 7-10 Site 2, 11-14 Sites 3 and 4, 15-18 Site 5, 19-25 Site 6). b) During 2010 and c) 2011, Site 5 included two additional sample locations that were submerged during 2009. During 2011, habitat variables were recorded during each of the three sample visits. Advancing ground cover was predominantly an upstream phenomenon, which had a negative effect on the extent of bare sediment.

Appendix 4 Specialist profile of species recorded during three years across six ERS sites on the Usk river system, Wales, UK, summarising the ERS specialists and other early succession specialists (Fowles 2004). Where evidence was unavailable, an assumption of habitat preference has been made.

Species	**Habitat preference**	**ERS specialist?[1]**	**Early succession habitat?**	**Reference**
Amara aenea (De Geer)	Dry grasslands, waste	X	✓	(Van Looy *et al.* 2007); (Saska and Honek 2003); (Jaskula and Soszynska-Maj 2011)
Amara sp	Generally on sand, fine gravel	X	✓	(Saska and Honek 2003);(Jaskula and Soszynska-Maj 2011)
Agonum lugens (Duftschmid)	Silt	X	✓	(Bouchard *et al.* 1998)
A.muelleri (Herbst)	Grasslands, open woodland	X	x	(Jaskula and Soszynska-Maj 2011)
B.atrocaeruleum (Stephens)	Shingle	✓	✓	(Van Looy *et al.* 2007)
B.decorum (Zenker in Panzer)	Sand and gravel	✓	✓	(Van Looy *et al.* 2007)
B.dentellum (Thunberg)	Muds, marshes	✓	x	Assumption
B.guttala (Fabricius)	Ubiquitous	X	x	Assumption
B.lunatum (Duftschmid)	Silty river banks	✓	x	Assumption
B.monticola (Sturm)	Gravel	✓	✓	Assumption
B.prasinum (Duftschmid)	Shingles and cobbles	✓	✓	(Andersen 2011a)
B.properans (Stephens)	Dry, open clay soils	X	✓	(Traugott 1998)
B.punctulatum (Drapiez)	Gravel and shingle	✓	✓	(Van Looy *et al.* 2007)
B.tetracolum (Say)	Open damp soil	X	✓	Assumption
B.tibiale (Duftschmid)	Gravel and shingle	✓	✓	Assumption
Bracteon littorale (Olivier)	Sand, fine gravel	X	✓	Assumption
Chlaenius vestitus (Paykull)	Mud and clay cracks	✓	x	(del Camino Pelaez and Salgado 2007)
Clivina collaris (Herbst)	Clay, sand, silt	✓	✓	Assumption
Harpalus rufipes (De Geer)	Open dry soils	X	✓	(Zhang *et al.* 1997)
Nebria brevicollis (Fabricius)	Ubiquitous	X	x	(Noordhuis *et al.* 2001; Jaskula and Soszynska-Maj 2011)
Paranchus albipes (Fabricius)	Freshwater margins	X	x	Assumption
Patrobus atrorufus (Ström)	Upland habitats and woodland	X	x	Assumption
Platynus assimilis (Paykull)	Woodland	X	x	(Kivimagi *et al.* 2009)
Pterostichus melanarius (Illiger)	Gardens, grassland, crops	X	x	(Noordhuis *et al.* 2001; Jaskula and Soszynska-Maj 2011)
P.nigrita (Paykull)	Most damp lowland habitats	X	x	(Jaskula and Soszynska-Maj 2011)
P.vernalis (Panzer)	Most damp lowland shaded habitats	X	x	(Jaskula and Soszynska-Maj 2011)
Trechus quadristriatus (Schrank)	Widespread	X	x	(Jaskula and Soszynska-Maj 2011)
Larva	Gravel, shingle, cobbles	✓	✓	Assumption

Appendix 5 Beetle dataset for completely randomised block experiment at two ERS sites on the Usk river system Wales, UK, 2013.

Date (for time reference)	Site	Time	Cell ref	Distance from water (m)	Food	Leaf litter	*B. atrocaeruleum*	*B. decorum*	*B. prasinum*	*B. punctulatum*	*B. tetracolum*	*B. tibiale*	*B. quadrimaculatum*	*B. properans*	*Paranchus albipes*	*A. muelleri*	*Pterostichus melanarius*	*P. vernalis*	*Sinuchus vivalis*	*Trechus quadristriatus*	*Amara sp.*	Larvae	Species richness	Beetle abundance
08/06/2013	1	1	3a	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
08/06/2013	1	1	3b	2	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
08/06/2013	1	1	3c	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
08/06/2013	1	1	2a	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
08/06/2013	1	1	2b	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
08/06/2013	1	1	2c	3	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
08/06/2013	1	1	1a	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
08/06/2013	1	1	1b	4	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
08/06/2013	1	1	1c	4	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
08/06/2013	6	1	3a	1.5	2	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	15
08/06/2013	6	1	3b	1.5	1	1	11	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	12
08/06/2013	6	1	3c	1.5	2	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11
08/06/2013	6	1	2a	2.5	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
08/06/2013	6	1	2b	2.5	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
08/06/2013	6	1	2c	2.5	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	5
08/06/2013	6	1	1a	3.5	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
08/06/2013	6	1	1b	3.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
08/06/2013	6	1	1c	3.5	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
15/06/2013	1	2	3a	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
15/06/2013	1	2	3b	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	1	2	3c	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	1	2	2a	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
15/06/2013	1	2	2b	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	1	2	2c	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	1	2	1a	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	1	2	1b	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	1	2	1c	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	6	2	3a	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 5 Beetle dataset for completely randomised block experiment at two ERS sites on the Usk river system Wales, UK, 2013.

Date (for time reference)	**Site**	**Time**	**Cell ref**	**Distance from water (m)**	**Food**	**Leaf litter**	***B. atrocaeruleum***	***B. decorum***	***B. prasinum***	***B. punctulatum***	***B. tetracolum***	***B. tibiale***	***B. quadrimaculatum***	***B. properans***	***Paranchus albipes***	***A. muelleri***	***Pterostichus melanarius***	***P. vernalis***	***Sinuchus vivalis***	***Trechus quadristriatus***	***Amara sp.***	**Larvae**	**Species richness**	**Beetle abundance**
15/06/2013	6	2	3b	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	6	2	3c	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	6	2	2a	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	6	2	2b	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	6	2	2c	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	6	2	1a	1	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	2
15/06/2013	6	2	1b	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15/06/2013	6	2	1c	1	2	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	2
29/06/2013	1	3	3a	2.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
29/06/2013	1	3	3b	2.5	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
29/06/2013	1	3	3c	2.5	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
29/06/2013	1	3	2a	3.5	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
29/06/2013	1	3	2b	3.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29/06/2013	1	3	2c	3.5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29/06/2013	1	3	1a	4.5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
29/06/2013	1	3	1b	4.5	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
29/06/2013	1	3	1c	4.5	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29/06/2013	6	3	3a	1	2	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	21
29/06/2013	6	3	3b	1	1	1	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9
29/06/2013	6	3	3c	1	2	1	11	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	13
29/06/2013	6	3	2a	2	1	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	13
29/06/2013	6	3	2b	2	1	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7
29/06/2013	6	3	2c	2	0	2	16	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	17
29/06/2013	6	3	1a	3	0	2	10	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	11
29/06/2013	6	3	1b	3	0	2	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9
29/06/2013	6	3	1c	3	2	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7
06/07/2013	1	4	3a	3	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5
06/07/2013	1	4	3b	3	1	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	10

Appendix 5 Beetle dataset for completely randomised block experiment at two ERS sites on the Usk river system Wales, UK, 2013.

Date (for time reference)	Site	Time	Cell ref	Distance from water (m)	Food	Leaf litter	*B. atrocaeruleum*	*B. decorum*	*B. prasinum*	*B. punctulatum*	*B. tetracolum*	*B. tibiale*	*B. quadrimaculatum*	*B. properans*	*Paranchus albipes*	*A. muelleri*	*Pterostichus melanarius*	*P. vernalis*	*Sinuchus vivalis*	*Trechus quadristriatus*	*Amara sp.*	Larvae	Species richness	Beetle abundance
06/07/2013	1	4	3c	3	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
06/07/2013	1	4	2a	4	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
06/07/2013	1	4	2b	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
06/07/2013	1	4	2c	4	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6
06/07/2013	1	4	1a	5	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	10
06/07/2013	1	4	1b	5	2	2	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11
06/07/2013	1	4	1c	5	2	1	12	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	3	15
06/07/2013	6	4	3a	3	2	0	17	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	3	20
06/07/2013	6	4	3b	3	1	1	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	3	4	7
06/07/2013	6	4	3c	3	2	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	6
06/07/2013	6	4	2a	4	1	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	31
06/07/2013	6	4	2b	4	1	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	13
06/07/2013	6	4	2c	4	0	2	8	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	9
06/07/2013	6	4	1a	5	0	2	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	10
06/07/2013	6	4	1b	5	0	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7
06/07/2013	6	4	1c	5	2	1	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	16
12/07/2013	1	5	3a	1	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5
12/07/2013	1	5	3b	1	1	1	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8
12/07/2013	1	5	3c	1	2	2	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9
12/07/2013	1	5	2a	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
12/07/2013	1	5	2b	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
12/07/2013	1	5	2c	2	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
12/07/2013	1	5	1a	3	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6
12/07/2013	1	5	1b	3	2	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6
12/07/2013	1	5	1c	3	2	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6
12/07/2013	6	5	3a	1	2	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	2	14
12/07/2013	6	5	3b	1	1	1	6	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4	3	11
12/07/2013	6	5	3c	1	2	1	8	0	0	0	0	0	0	0	0	0	2	0	0	0	0	4	3	14

Appendix 5 Beetle dataset for completely randomised block experiment at two ERS sites on the Usk river system Wales, UK, 2013.

Date (for time reference)	Site	Time	Cell ref	Distance from water (m)	Food	Leaf litter	*B. atrocaeruleum*	*B. decorum*	*B. prasinum*	*B. punctulatum*	*B. tetracolum*	*B. tibiale*	*B. quadrimaculatum*	*B. properans*	*Paranchus albipes*	*A. muelleri*	*Pterostichus melanarius*	*P. vernalis*	*Sinuchus vivalis*	*Trechus quadristriatus*	*Amara sp.*	Larvae	Species richness	Beetle abundance
12/07/2013	6	5	2a	2	1	0	63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	65
12/07/2013	6	5	2b	2	1	0	21	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	22
12/07/2013	6	5	2c	2	0	2	22	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	3	24
12/07/2013	6	5	1a	3	0	2	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	41
12/07/2013	6	5	1b	3	0	2	54	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	55
12/07/2013	6	5	1c	3	2	1	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	26
20/07/2013	1	6	3a	5	0	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11
20/07/2013	1	6	3b	5	1	1	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	17
20/07/2013	1	6	3c	5	2	2	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	38
20/07/2013	1	6	2a	6	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
20/07/2013	1	6	2b	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
20/07/2013	1	6	2c	6	1	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8
20/07/2013	1	6	1a	7	1	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7
20/07/2013	1	6	1b	7	2	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7
20/07/2013	1	6	1c	7	2	1	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9
20/07/2013	6	6	3a	4.5	2	0	52	0	0	0	1	0	0	0	3	0	0	0	0	0	0	5	4	61
20/07/2013	6	6	3b	4.5	1	1	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	12
20/07/2013	6	6	3c	4.5	2	1	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	17
20/07/2013	6	6	2a	5.5	1	0	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	42
20/07/2013	6	6	2b	5.5	1	0	31	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	3	33
20/07/2013	6	6	2c	5.5	0	2	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	28
20/07/2013	6	6	1a	6.5	0	2	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	42
20/07/2013	6	6	1b	6.5	0	2	26	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	3	28
20/07/2013	6	6	1c	6.5	2	1	23	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	3	25
27/07/2013	1	7	3a	5	0	1	22	0	0	1	0	0	0	0	4	0	0	1	1	0	0	17	6	46
27/07/2013	1	7	3b	5	1	1	26	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	3	29
27/07/2013	1	7	3c	5	2	2	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	24
27/07/2013	1	7	2a	6	0	2	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	32

Appendix 5 Beetle dataset for completely randomised block experiment at two ERS sites on the Usk river system Wales, UK, 2013.

Date (for time reference)	**Site**	**Time**	**Cell ref**	**Distance from water (m)**	**Food**	**Leaf litter**	***B. atrocaeruleum***	***B. decorum***	***B. prasinum***	***B. punctulatum***	***B. tetracolum***	***B. tibiale***	***B. quadrimaculatum***	***B. properans***	***Paranchus albipes***	***A. muelleri***	***Pterostichus melanarius***	***P. vernalis***	***Sinuchus vivalis***	***Trechus quadristriatus***	***Amara sp.***	**Larvae**	**Species richness**	**Beetle abundance**
27/07/2013	1	7	2b	6	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	34
27/07/2013	1	7	2c	6	1	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	31
27/07/2013	1	7	1a	7	1	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	17
27/07/2013	1	7	1b	7	2	2	30	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	3	33
27/07/2013	1	7	1c	7	2	1	71	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	72
27/07/2013	6	7	3a	4	2	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6
27/07/2013	6	7	3b	4	1	1	30	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	4	33
27/07/2013	6	7	3c	4	2	1	16	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	18
27/07/2013	6	7	2a	5	1	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	13
27/07/2013	6	7	2b	5	1	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	20
27/07/2013	6	7	2c	5	0	2	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	27
27/07/2013	6	7	1a	6	0	2	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	31
27/07/2013	6	7	1b	6	0	2	22	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	24
27/07/2013	6	7	1c	6	2	1	31	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	32
02/08/2013	1	8	3a	4	0	1	9	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	10
02/08/2013	1	8	3b	4	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
02/08/2013	1	8	3c	4	2	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
02/08/2013	1	8	2a	5	0	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6
02/08/2013	1	8	2b	5	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
02/08/2013	1	8	2c	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
02/08/2013	1	8	1a	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
02/08/2013	1	8	1b	6	2	2	2	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	4	6
02/08/2013	1	8	1c	6	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
02/08/2013	6	8	3a	3.5	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2
02/08/2013	6	8	3b	3.5	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	3	3
02/08/2013	6	8	3c	3.5	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
02/08/2013	6	8	2a	4.5	1	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	4
02/08/2013	6	8	2b	4.5	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	6

Appendix 5 Beetle dataset for completely randomised block experiment at two ERS sites on the Usk river system Wales, UK, 2013.

Date (for time reference)	**Site**	**Time**	**Cell ref**	**Distance from water (m)**	**Food**	**Leaf litter**	***B. atrocaeruleum***	***B. decorum***	***B. prasinum***	***B. punctulatum***	***B. tetracolum***	***B. tibiale***	***B. quadrimaculatum***	***B. properans***	***Paranchus albipes***	***A. muelleri***	***Pterostichus melanarius***	***P. vernalis***	***Sinuchus vivalis***	***Trechus quadristriatus***	***Amara sp.***	**Larvae**	**Species richness**	**Beetle abundance**
02/08/2013	6	8	2c	4.5	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	4
02/08/2013	6	8	1a	5.5	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
02/08/2013	6	8	1b	5.5	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
02/08/2013	6	8	1c	5.5	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
					Total per species:		**1514**	**7**	**2**	**4**	**7**	**4**	**1**	**1**	**18**	**3**	**6**	**2**	**1**	**1**	**1**	**81**	**16**	**1653**