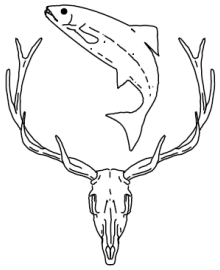
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LETTEREWE

Red deer habitat management in the Highlands: Consequences for invertebrates

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Abstract

In Scotland, the well documented increase in the red deer population is widely regarded as a cause for concern, due to potentially detrimental impacts of grazing. This has lead to conflicting objectives between conservation and deer managers, despite the extent of the increase and the resulting impact both being hotly debated issues. Upland heather moorland is of international conservation importance while woodland habitats are some of the most stable ecosystems in anthropogenic landscapes. In the UK oak woodland plays a crucial role in the maintenance of biodiversity, and both heather moorland and oak woodland may be subject to degradation or decline due to grazing. This study is based in north-west Scotland, and investigates the consequences of two deer management strategies, in two habitat types, for invertebrates. An observational study of heather moorland under two extremes of grazing pressure provided little evidence for negative impacts of grazing on invertebrates on the more heavily grazed Letterewe Estate, suggesting that the deer population is not a cause for concern in terms of invertebrate biodiversity. An experimental study of grazed and un-grazed oak woodland found some positive effects, and no instances of negative grazing impacts on invertebrate biodiversity, and no effect on guild structure. This work highlights the need for science to inform land management policy that must often seek to balance conservation objectives with economic interests, and supports the notion that a red deer herd of a size consistent with viable stalking interests can be integral to the maintenance of biodiversity and the natural heritage.

Declaration of originality

I conducted various pilot studies for Chapters Three, Four and Five, but the bulk of the data for Chapter Three was collected by an MSc. student working under my supervision. Donald Quicke identified parasitoids, Roger Morris identified hoverflies, and Richard Adu-Acheampong carried out the initial sorting of the malaise trap samples. The Letterewe oak woodland grazing exclosures used in Chapters Four and Five are a joint venture between the estate and Scottish Natural Heritage. All other work is my own, or referenced appropriately.

Paul James Tinsley-Marshall

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Units

α = log series diversity index α

cm = centimetres

ha = hectares

km = kilometres

m = meters

mm = millimetres

pH = measure of the acidity or basicity of a solution

Abbreviations

BAP = Biodiversity Action Plan

EU = European Union

GLM = Generalised Linear Model

NNR = National Nature Reserve

NVC = National Vegetation Classification

SAC = Special Area of Conservation

SNH = Scottish Natural Heritage

SSSI = Site of Special Scientific Interest

Chapter 1
General introduction

1.1 Red deer in the Highlands

Issues surrounding deer numbers in the UK, particularly in Scotland, and their impacts on the ecology of their habitats have been well documented (Milner *et al.*, 2002, Clutton-Brock *et al.*, 2004a, Virtanen *et al.*, 2002). Particular attention has been paid to Letterewe Estate in the Highlands (Milner *et al.*, 2002). The red deer *Cervus elaphus* population in Scotland has increased from 300,000 in 1989, to 450,000 in 2002 (Clutton-Brock *et al.*, 2004a), and historically this has been due in part to the loss of natural predator control mechanisms (Nilsen et al., 2007). The issues with which increased deer numbers have been associated include degradation of heather dominated moorland communities, prevention of regeneration in native woodland, and damage to forestry and agriculture (Clutton-Brock *et al.*, 2004a). Deer and other wild and domestic ungulates have been an important factor in the shaping of habitats currently seen in the UK (Stewart, 2001, Vera, 2000) and their impact is largely though grazing and browsing while feeding on plants. Despite a large body of research supporting the view that the rise in red deer numbers is having a detrimental effect on heather moorland habitats, some researchers believe the rise in numbers and associated impacts have been over estimated (Clutton-Brock *et al.*, 2004a). These authors point to the unreliability of counting methods for animals in woodland, and calculate a much more gradual population increase than has previously been put forward. Nevertheless, deer are implicated in a range of conservation issues, and field experiments are required to quantify their impacts.

1.1.1 Red deer management: consequences for invertebrates

Understanding invertebrate species assemblages and factors that influence them is a central question in ecology. Grazing and browsing by herbivores impact invertebrate assemblages through their effects on the composition, structure and dynamics of vegetation (Crawley, 1983, Morris and Plant, 1983). Much has been published on the impact of domestic

livestock in agricultural systems and wild grazing ungulates in commercial forestry. The impact of wild grazing mammals such as red deer, in natural habitats, is much less known. Deer can be manipulated in a variety of ways to accomplish various land management objectives. Here the consequences of two deer management strategies on the invertebrate assemblages of two habitat types were investigated.

1.1.2 The ecology of grazing and browsing

The actions of large herbivores have been an important component in shaping terrestrial habitats and these animals are often described as ecosystem engineers (Cote, 2004, Jones *et al.*, 1994, Vera, 2000). Large herbivores such as deer feed by grazing and browsing, which can have significant effects on vegetation (Mysterud, 2006) from individual plant to landscape scales (Hobbs 1969, Augustine & McNaughton, 1998). Behavioural characteristics such as selective foraging, predation avoidance, and shelter requirements, dictate that their impact is heterogeneous within plant communities at different spatial and temporal scales (Kielland and Bryant 1998, Allison 1990, Price 1991, Schmitz 2003, Letourneau and Dyer 2004) resulting in varied consequences for vegetation physiognomy, composition and ecological function (Pastor and Naiman 1992, Jefferies et al 1994, Dannel et al 2003). Plants vary in their response and susceptibility to grazing and browsing. For instance woody plants such as trees and shrubs may extend at least some of their biomass out of the reach of herbivores, while canopy architecture may influence foraging efficiency through variation in the density of shoots (Renaud et al 2003). Browsing can alter the shape of the tree canopy and assemblage in space and time, the strongest effect being through selective browsing on young trees, influencing the eventual composition of the mature stand. In woodland habitats herbivores also cause damage though bark stripping and fraying, trampling and removal of the understory (Gill 1992). Herbs are smaller, putting them within reach of herbivores, shorter lived, and allocate a greater proportion of their biomass to photosynthetic tissue than trees. This gives them a greater capacity for growth, but lower recovery from grazing. Gramminoids differ fundamentally from dicotyledonous plants in that growth occurs from meristems situated close to the ground. This places them within the protection of old leaf sheaths and below the optimal grazing level for the majority of herbivores, putting them among some of the most grazing tolerant plants (Crawley, 1983).

Studies on the impacts of grazing and browsing have reported both positive and negative effects on biodiversity. There seems to be no general consensus due to the variety

of systems studied and the varied impacts that grazing and browsing have, however it is accepted that large herbivores can have a profound effect on plant community structure, and that losses in terms of biodiversity are not only intrinsic, but can lead to a cascade of effects on other species. This is particularly true with regard to invertebrates which form important links between primary producers and predators, at all trophic levels, and are important components of nutrient cycles, plant propagation, maintenance of plant community structure, and composition, food for insectivorous vertebrates and invertebrates, and in maintaining animal community structure (Gullan and Cranston, 2000).

1.1.3 The red deer diet

Red deer are selective feeders (Fraser and Gordon, 1997) and select their diet in accordance with the intake rate maximising principle (van Wieren, 1996). They eat a mixed diet of at least 145 plant species which varies with habitat (Gebert and Verheyden - Tixier, 2001), season and geography (Stewart, 2001). Food categories include coniferous trees, leaves of deciduous trees and shrubs, *Rubus, Calluna* and *Vaccinium,* leaves of other dwarf-shrubs, twigs and bark, forbs, seeds and fruit, cultivated forbs, concentrate food, grasses and sedges, ferns, mosses, lichens and fungi, and others. The four main components are grasses and sedges, 29.6 %, at a proportion of 1/3 in all habitats, *Calluna* and *Vaccinium* 23.3 %, eaten mainly in moorland and infrequently in deciduous woodland, leaves of deciduous trees & shrubs 10.2 %, predominantly in deciduous woodland, and conifers 8.8 %, consumed in coniferous woodland. Oak, Willow and aspen are preferred browse species, while Yew and Holly are generally avoided (Stewart, 2001) although Holly not so at Letterewe. Seasonal variation occurs (Dumont *et al* 2005, Fraser and Gordon 1997, Latham *et al* 1999) such as when seed and fruit items are available (Gebert and Verheyden - Tixier, 2001). Diet selection may be either proportionate (Latham *et al* 1999) or disproportionate (Milner *et al* 2002) with respect to availability of particular food resources (Stewart, 2001).

1.1.4 Grazing, browsing and plants

Both large and small mammalian herbivores can have significant impacts on vegetation communities. Large wild herbivores in particular are recognised as historically important in structuring current woodland ecosystems (McEvoy *et al.*, 2006, Putman, 1996), but also as damaging pests in agriculture, horticulture, forestry and woodlands (Putman and Moore, 1998). Natural regeneration of woodlands can however be entirely prevented by the presence of herbivores, although in areas where sheep and red deer graze woodlands, there is evidence that the former have a much greater impact on regeneration (Putman, 1996). At

Letterewe Estate in the Scottish Highlands there is no regeneration in the Atlantic oak woodland outside of grazing exclosures due to grazing pressure from red deer (Milner *et al.*, 2002). Complete exclusion of livestock will often allow adequate regeneration to occur (Pigott, 1983) although with careful consideration of stocking densities and forage availability, regeneration can occur in managed grazed woodlands (Pollock et al., 2005). Scottish pine woodlands grazed by red deer had reduced heather, increased grass, and unchanged bilberry cover in a study documented by Baines *et al.,* (1994). Bilberry was however 50% shorter and had twice the number of apical tips removed in grazed woodlands. Exclusion of red deer grazing had a negative effect on productive plant communities on the Scottish island of Rùm, causing considerable decline in species richness (Virtanen *et al.*, 2002). The authors suggest that grazing maintains plant species diversity of productive plant communities, and found the effect of reduced grazing pressure on unproductive communities to be insignificant. In a study of sub-alpine grasslands, plant species richness was increased in red deer grazed areas (Schutz et al., 2003). Livestock grazing in woodlands can increase plant diversity, and the abundance of ruderal species, and may decrease the abundance of competitively dominant species (McEvoy et al., 2006). In a temperate sub-humid grassland Altesor *et al.,* (2006) found that plant species richness was higher in grazed than un-grazed plots. Rabbit grazing may affect seedling recruitment of some grassland species (Edwards and Crawley, 1999), a mechanism that will affect plant species composition. Grazing on moorland may reduce cover (Hartley and Mitchell, 2005) and chemical composition and production (Moss, 1981) of the dominant *Calluna* vegetation in this habitat, where the predominant grazers are red deer, sheep and mountain hares, particularly in Scotland (Hewson, 1976). The extent of heather loss due to grazing is such that heathland communities may be lost altogether and replaced by rough grassland, a considerable conservation concern (Thompson, 1995). This process is most often associated with sheep grazing where animals are present at higher stocking densities than deer will naturally reach (Dodgshon and Olsson, 2006). Soil disturbance caused by trampling may serve to provide micro-sites which allow seedling recruitment of otherwise competitively excluded plants (Bokdam and Gleichman, 2000) or may have detrimental impacts such as those seen in Scandinavian lichen heath (Mysterud, 2006). Excreta produced by large herbivores can increase soil nutrient content (Frank and McNaughton, 1993) or pH (Frank, 2008) with significant effects on vegetation. Heavy grazing may decrease primary productivity, however lighter grazing may stimulate growth and production, consequently it

is advisable to be cautious when generalising about the potential effects of grazing on biodiversity (Olofsson *et al.*, 2001).

1.1.5 Grazing as a driver of diversity

There are various mechanisms by which grazing and browsing impact invertebrate communities through effects on vegetation, for example by driving botanical diversity, growth, structure and biomass (Crawley, 1983; Lawton, 1983; Siemann, 1998; Rambo, 1999; Virtanen, 2002; Gonzalez-Megias, 2004). Mechanisms include disruption of competitive hierarchy and alteration of light penetration through the canopy (Rambo and Faeth, 1999). Invertebrate diversity has often been predicted to be a function of botanical diversity (May, 1990; Hunter and Price, 1992) where high levels of α-diversity in plants lead to high levels of α-diversity in higher trophic levels. The theory that a greater number of resources will support increased abundances of consumer species is supported in studies that show a link between botanical and invertebrate herbivore diversity (Southwood et al., 1979; Lawton, 1983; Tscharntke, 1997; Siemann, 1998; Siemann et al., 1998; Rambo, 1999; Koricheva et al., 2000; Gonzalez-Megias, 2004). Potential exists for a cascade of effects to higher trophic levels, for example by increasing the availability and diversity of floral resources utilised by parasites and predators (Price et al., 1980) or altering their foraging efficiency (Coll and Bottrell, 1996). Another consequence of increased plant species (Tilman et al., 1996) or functional diversity (Tilman et al., 1997) is an associated increase in productivity which can lead to elevated invertebrate abundance (Siemann, 1998). Top down effects exerted by predators and parasites may drive a system of trade-offs between susceptibility and competitive ability in invertebrates that maintain higher levels of herbivore diversity than would exist in the absence of such pressure (Menge and Sutherland, 1976; Leibold, 1996).

Ecological theory predicts increased invertebrate diversity with increasing vegetation structural complexity (Lawton and Schroder, 1977, Southwood *et al.*, 1979). The structural diversity or architecture of plant communities is thought to be correlated with both botanical species, and functional group diversity (Siemann, 1998) which in turn may be correlated with invertebrate assemblage characteristics. The response of invertebrates to architectural diversity is such that invertebrate diversity is maintained or continues to increase even after botanical diversity has declined (Southwood et al., 1979). Plant architecture is described in a review by Lawton (1983) as pertaining to a suite of plant characteristics including size, growth form, seasonality, persistence and variety of above-ground structures. The

relationship between plant architecture and phytophagous insect diversity is discussed and a variety of hypotheses proposed. The positive relationship between plant architectural complexity and the abundance of invertebrate herbivores is due to increased niche availability (Strong *et al.*, 1984). Grassland swards are subjected to structural modification by agricultural practises including grazing that may reduce resource availability and microclimatic conditions to the detriment of invertebrates (Purvis and Curry, 1981). With the correct management strategy however, sward architecture can be managed to benefit phytophagous invertebrates directly and predatory invertebrates indirectly (Woodcock *et al.*, 2007a, Woodcock *et al.*, 2007b). These studies refer to grassland swards, however another example is found in *Calluna vulgaris* which supports a large number of larval Lepidoptera species, the diversity of which increases with increasing plant height (Haysom and Coulson, 1998).

Where habitat modification by grazing and browsing alters vegetation species, architectural or functional diversity, a cascade of impacts to the higher invertebrate trophic levels and beyond may be expected. These mechanisms work to increase heterogeneity within habitats, creating and increasing the number of available niches, thereby the presence and activity of herbivores acts positively on invertebrate diversity. Above some critical threashold of grazing and browsing pressure, these positive effects may start to negatively impact diversity, through the homogenisation of vegetation structure, direct food competition, and a reduction in the number of available niches. Many studies report detrimental effects on invertebrate groups as a result of grazing and browsing pressure.

1.1.6 Grazing, browsing and invertebrates

A large proportion of biodiversity consists of ecologically important but understudied taxa, many of which are invertebrates (May 1988). As the most species rich group they occupy a huge number of niches. Consequently it can be expected that there are numerous potential ways in which herbivores might affect invertebrate animals, both directly and indirectly. The impact of deer on woodland invertebrates can be broken down into four categories: 1. Direct competition for food with herbivorous invertebrates; 2. Indirect effects caused by changes to species composition, biomass or quality of vegetation; 3. Indirect effects due to modification of the physical habitat structure; 4. Direct effects on communities of deer commensals and parasites, and on coprophagous invertebrates associated with deer dung (Stewart, 2001). Examples include changes in the quality and quantity of resources such as litter, dead wood, seeds, flowers, oviposition and nesting sites, and the structure of

vegetation. The presence of the living and dead bodies of herbivores in ecosystems is conducive to a variety of relationships, both species specific, such as deer keds *Lipotena cervi* and ticks *Ixodes scaularis*, and non-specific such as carrion feeding Coleoptera such as *Necrophorus vespiloides* and many Diptera. Excreta provide resources for a diverse assemblage of coprophages that either feed or oviposit on dung (Stewart, 2001, Andresen and Laurance, 2007, Gibson, 1992a) and while many of these are generalist, some are primarily specific to individual species of herbivore dung (Duncan et al., 2001). The abundance of coprophages has been shown to fluctuate in response to herbivore density (Putman et al., 1989) and human and elephant induced disturbance were found to affect dung beetle assemblage structure in Sand Forest in southern and South Africa (Botes et al., 2006). Changes in the quality and distribution of dung, as well as habitat structure were implicated. Hunting of mammals can affect the availability of resources for dung-feeders (Andresen and Laurance, 2007) and the available biomass of mammal carcasses for carrion feeding beetles (Smith and Merrick, 2001). Nutrient addition to soils through urine and dung can affect microbial activity, content of organic carbon, and total nitrogen content (Mohr et al., 2005). Many invertebrates require specific microclimatic conditions as their comparatively small body size makes them more susceptible to fluctuations in moisture and temperature levels than larger organisms (Gullan and Cranston, 2000). The microclimatic conditions of their habitat might therefore be expected to influence their ability to survive within habitat patches. Temperature levels may be affected by the amount of light penetrating a vegetative canopy, and moisture by the level of wind, influenced by the density of vegetation. In a cattle grazing experiment, grasshopper abundance was higher in un-grazed plots which had cooler, shadier, less windy, and more humid microclimates than grazed plots (O'Neill et al., 2003). The larvae of some thermophylic butterflies require certain grazing densities to maintain a short sward that provides the appropriate microhabitat conditions for the food plant (Gibson, 1992a). In an Australian rainforest, beetle species composition was different in dry and wet forests, and species characteristic of dry forests were more abundant in small remnants of forest, and those characteristic of moister forests more so in larger remnants (Grimbacher et al., 2006). These observations were attributed to microclimate, rather than plant diversity, structure, patch size, or isolation effects. Trampling and localised patches of intensive grazing can create potential nest sites for ants (Gonzalez-Megias, 2004). The rarest invertebrate species in woodlands are often associated with early and late successional stages such as clearings and mature or senescent habitat patches, particularly dead and decaying wood. Where herbivores create or prolong

the presence of gaps, invertebrate diversity will benefit (Stewart, 2001). Many studies suggest that invertebrate diversity is maximised at intermediate herbivore densities (Di Giulio *et al.,* 2001; Swengel and Swengel, 2001) a theory compliant with the intermediate disturbance hypothesis (Grime, 1973b). Intermediate grazing densities benefit bees through the removal of competitive occlusion of floral resources by non-flowering vegetation, whereas overgrazing will remove these also (Sjodin et al., 2008). Species richness of soil dwelling *Acari* was higher in grazed than un-grazed plots in a sub-humid grassland (Altesor et al., 2006). Spiders are sensitive to changes in habitat structure (Duffey, 1993; Uetz, 1991) and may exhibit microhabitat preferences that maximize prey capture and minimize predation (Edgar, 1971). Herbivores might therefore be expected to impact araneaen communities and low intensity grazing to maximize diversity (Bell *et al.*, 2001). Spider responses to grazing may be complex, either being reduced with increased grazing intensity, or more explicitly dependent on the presence of specific plant species, where these are important structures for large web building species (Gibson, 1992b). Web building spiders differ fundamentally from pursuit predators in the sedentary ambush nature of their prey capture behavior, and therefore also in the nature of their reliance on plant structures.

Over three quarters of resident breeding butterflies in the UK are dependent on habitats maintained to some extent by grazing, though effects on the structure and composition of vegetation communities (Feber, 2001). Grazing maintains the short sward required by the silver spotted skipper *Hesperia comma*, varied sward structure and larval food plant density required by the marsh fritillary *Eurodryas aurinia,* and open bracken patches in woodland that are a necessity of the pearl-boarded fritillary *Boloria euphrosyne.* Conversely re-growth is under threat from rising deer numbers in important coppice woodland habitats.

Many studies have examined grazing impacts on invertebrates of domestic livestock in agricultural and natural grassland systems (Gibson, 1992a; Dennis, 1997; Rambo, 1999; Dennis, 2001; Cagnolo, 2002; Kruess, 2002b; Kruess, 2002a;Dennis, 2003; O'Neill et al., 2003; Dennis, 2004; Gonzalez-Megias, 2004; Cole, 2005), domestic livestock in heather moorland (Gardner, 1997; Hartley, 2003) and livestock (AbenspergTraun, 1996) and cervids in woodland (Suominen, 1999; Suominen et al., 1999a; Suominen et al., 1999b; Feber, 2001; Stewart, 2001; Suominen, 2003; Allombert et al., 2005b). Very few studies have experimentally examined the impacts of red deer in boreal forest (Melis *et al.*, 2006) and Scottish pinewoods (Baines *et al.*, 1994), and empirical data from deciduous woodland or heather moorland ecosystems is distinctly lacking. Baines *et al.,* (1994) found that grazing

exclosures had greater abundance of larval Lepidoptera, Formicidae, Coleoptera, Diptera, Areneae and Plecoptera than grazed plots and suggest possible implications for birds. The authors suggest that deer remove the growing tips of bilberry and therefore directly compete with Lepidoptera for food, or inadvertently predate eggs or larvae. Deer may also positively impact the abundance of leaf mining insects through effects on plant nutrient levels (Barret and Stilling 2006). Leaf miners were more abundant on high deer density islands in response to foliar nutrient levels, either preexisting or indirectly caused by dung deposition. Studies linking grazing and browsing effects on plants to associated effects on invertebrates have shown a reduction in insect herbivores on willow browsed by reindeer (Den Herder *et al.*, 2004), and increased abundance but reduced diversity and richness of insects in bilberry *Vaccinium myrtillus* grazed by red deer (Melis *et al.*, 2006). Browsing by beavers *Castor canadensis* can indirectly affect the abundance of leaf beetles attracted by the opportunity to sequester increased levels of plant defence chemicals produced in new growth stimulated by beaver browsing (Martinsen et al., 1998).

1.1.7 Grazing, browsing and birds

Little information is available in the current literature regarding the impacts of herbivores on birds, although theory predicts cascading effects of habitat modification or disturbance from both top down and bottom up effects. Fluctuations in the abundance of dung and carrion feeding invertebrates are associated with a cascade of effect on birds including tawny owls and corvids (Duncan et al 2001). Parasites carried by large herbivores provide food for cowbirds, and invertebrates disturbed by movement though vegetation are predated by the cattle egret *Bubulcus ibis* (Mayfield, 1965). Natural grasslands have often been modified in some way by anthropogenic activities and are frequently used for livestock grazing. Changes in vegetation structure and plant diversity have been shown to affect food and nest site availability for birds. In North American prairies grazing is implicated in the reduction of species richness and abundance of bird assemblages (Kantrud 1981; Chamberlain et al 2000; Gates and Donald 2000; Soderstrom *et al* 2001) and reduced nesting density and success of waterfowl (Klett *et al.,* 1988; Kirby *et al* 1992). Nests may be lost to trampling (Beintema and Muskens 1987; Barker *et al.,* 1999; Grant *et al.,* 1999), exposure to predation may be increased (Brua, 1999; Wilson and Harnett, 2001) and the supply of invertebrate food decreased (Soderstrom *et al.,* 2001). As with impacts on invertebrates, the reduced habitat heterogeneity caused by grazing is often the cause. A good example of this is illustrated in salt marshes which are often grazed during the summer (Norris *et al.*, 1998).

An intermediate level of grazing produced the most heterogeneous sward, and low to intermediate grazing was most beneficial to breeding redshank *Tringa totanus.* Heavy grazing lead to a short, dense and homogenous sward, and cessation of grazing to a tall rank sward, both of which were detrimental to breeding birds.

Sheep have in the past been a major component of grazing pressure in the UK and concerns about their impact on birds focus around reduction of preferred vegetation types, changes in food availability and alteration of predation dynamics (Fuller and Gough, 1999). Historical declines in bird populations have been attributed to increases in sheep grazing, however high levels of sheep grazing have conversely been demonstrated to facilitate the abundance of a largely insectivorous avian assemblage (Loe et al., 2007). Mixed low intensity livestock grazing by sheep and cattle in grassland was found to increase breeding density of the meadow pipit *Anthis pratensis* when compared to single species or un-grazed treatments (Evans *et al.*, 2006b). This effect is attributed to changes in prey abundance as a result of a more heterogeneous sward structure. Another possible mechanism by which grazing can affect bird populations has again been demonstrated in the meadow pipit (Evans et al., 2005). Eggs laid under high and zero sheep stocking densities were smaller than those laid under intermediate grazing pressure, although no link to fledging success was found.

Grazing also facilitates feeding opportunities for geese, by causing the development of short high quality swards (Van der Graaf *et al*., 2002; Stock and Hofeditz, 2000) which are used in preference to later successional stages that contain taller less attractive plant species. Invertebrates are an important component of the diet of many moorland birds, and are the exclusive constituent in many species (Buchanan, 2006). The mostly widely predated taxa include Arachnida, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Oligochaeta, of which the beetles and flies are the most important. The author suggests that a heterogeneous mosaic of habitat types and structures produces the greatest abundance of invertebrate prey and is of most benefit to birds. Heavy grazing by sheep and deer is associated with a decline in black grouse *Tetrao tetrix* breeding success (Baines, 1996). Low levels of grazing were considered beneficial to the development of taller vegetation cover that supported preferred invertebrate food species. Reduction of the understory is reported as a major factor in the decline of woodland bird species (Fuller, 2001, Martin and McIntye, 2007) particularly in those species that use bramble *Rubus fruticosus* (Perrins and Overall, 2001). Species substitution may cause apparently little change in avian richness in grazing treatments (McShea and Rappole 2000, Moser and Whitmer 2000, Fuller 2001) whereas other studies have shown a clear decline in avian

diversity in response to browsing (De Celesta 1994). A 93% decline in understory dependent birds was reported from the Haida Gwaii archipelago in islands with a long history of grazing by deer (Allombert *et al.*, 2005a). There was also a 55-70% reduction in songbird numbers and α diversity on islands where deer were present. Preferred foraging height predicted the susceptibility of bird species to grazing pressure in and Australian woodland (Martin and Possingham, 2005). The general trend in all habitats is that low to intermediate levels of grazing and browsing pressure result in the most favourable conditions for bird communities, although it is not clear from these studies what fraction of herbivore effects on birds is attributable to indirect effects acting through variation in invertebrate abundance and therefore availability of food for birds.

1.1.8 Grazing, browsing and mammals

Population levels of coprophagous invertebrates have been shown to impact woodland bats in the UK (Duncan *et al.,* 2001) potentially rendering them sensitive to changes in grazing herbivore numbers. In common with birds, changes in the understory structure in woodlands, or sward architecture in grasslands might be expected to influence the suitability of habitats for small mammals. For example, the field vole *Microtus agrestis* suffers population declines under sheep grazing (Evans *et al.*, 2006a) and cattle grazing can reduce the availability or quality of food, increase predation risk through structural impacts on vegetation, and trampling can affect the suitability of soil for burrowing by small mammals (Torre et al., 2007).

1.2 Rationale for this study

Upland heather moorland is of international conservation importance and is thought to be declining due to grazing pressure. In Scotland this includes 13 plant communities protected under the EC habitats directive, and the associated bird assemblage is of outstanding conservation value (Thompson, 1995). Invertebrates comprise approximately 65% of all organisms, provide good species diversity correlations, and are a significant component of ecosystem function (Schweiger *et al.,* 2005). Woodland habitats are some of the most stable ecosystems in anthropogenic landscapes, and in the UK oak woodland plays a crucial role in the maintenance of biodiversity. Ancient woodlands that have to some extent been contiguous since the end of the 18th century, and act as important reservoir habitats for relict plant and animal species (Sroka and Finch, 2006). Native Scottish woodlands in the Highland region comprise 35% of the total wooded area, compared to 100 % at the turn of the century, and grazing by deer and sheep is one of the main reasons for the lack of natural

regeneration in many wooded areas (Ings, 1999). There is some debate as to the origin of the Letterewe oak woodland, considered by some to be a relict fragment of the Atlantic oak woodland characteristic of the Western seaboard of Europe. The even age and height structure of the stand however, is consistent with the historical industrial use of the woodland in the iron smelting industry. Nevertheless, the importance of the Letterewe oak wood for biodiversity is highlighted by its inclusion in the Ardlair-Letterewe Special Area for Conservation (SAC) and Site of Special Scientific Interest (SSSI) designations. Both habitat types may be subjected to degradation or decline due to grazing pressure. The well documented increase in the red deer population has been widely implicated as having a detrimental effect on habitats, although the extent of the increase and the resulting impact are highly debated issues. Pressure from conservation bodies demands that deer managers must seek to balance conservation priorities with the economic constraints of land stewardship and sporting interests. Empirical studies are required to determine the effects of grazing and browsing in specific habitats and under individual grazing regimes in order to develop and inform management and conservation policy. This review of the literature clearly demonstrates that a blanket approach with regard to the effects of grazing and browsing will not always be appropriate for the maximisation of biodiversity and conservation priorities. Quantifying the effects of deer grazing on community composition of a range of taxa is vital to our understanding of the real impacts of deer on biodiversity.

1.3 Thesis layout

This thesis examines the role of two deer management strategies in influencing invertebrate assemblages, in two habitat types. Chapter Three investigates the impact of heavy deer culling on invertebrates in upland heather moorland. A National Nature Reserve (NNR) managed under a heavy deer culling policy for conservation objectives is compared with an estate holding commercial stalking deer densities. Chapter Four uses a grazing exclusion experiment to look at the role of deer exclusion on invertebrate abundance, richness and diversity in oak woodland, and the same experiment is used in Chapter Five to look at exclusion effects on guild responses, the ecological functionality of deer dung removal by invertebrates, and its interaction with grazing management.

Chapter 2

Materials and methods

2.1 Study site

Letterewe Estate (57° 42´N, 5° 25´W) is a privately owned tract of land in Wester Ross, in the north-west Highlands of Scotland. In total the estate covers an area of approximately 32,000 ha and is managed predominantly for deer stalking interests and conservation priorities. Altitude ranges from sea level to over 1000 m, and the terrain is rugged and dramatic. Open moorland characterised by wet heath vegetation is the dominant habitat type over most of the estate. The northern shore of Loch Mare supports Atlantic oak woodland, which forms part of the Ardlair - Letterewe Site of Special Scientific Interest (SSSI). Beinn Eighe (57° 36.5´N, 5° 22.4´W) is a national nature reserve (NNR) managed by Scottish Natural Heritage (SNH) for conservation objectives. It is predominantly open moorland with similar plant communities to those found at Letterewe. In addition it also contains the largest fragment of ancient Caledonian pinewood in north-west Scotland which it was originally set up to protect. On both estates, red deer *Cervus elaphus* are the primary vertebrate herbivore and in the absence of rabbits *Oryctolagus cuniculus* make the dominant contribution to mammalian grazing pressure. Other species including mountain hares *Lepus timidus,* red grouse *Lagopus lagopus scotica,* ptarmigan *Lagopus mutus.* Roe deer *Capreolus capreolus,* Sika deer *Cervus nippon* and feral goats *Capra hircus* make a limited contribution. Red deer are managed through stalking to maintain a population density of approximately 15 per 100 ha at Letterewe (Milner *et al.*, 2002). Over the duration of this study densities at Beinn Eighe averaged 2.63 per 100 ha, although in 2010 the four year average is now 4.6 per 100 ha (personal communication: T. Doe (SNH)). At both sites grazing exclosures are employed to facilitate natural regeneration of trees. A detailed account of the climate can be found in Milner *et al.,* (2002). It is typical of the region, with much rain, wind, and mild temperatures. Local variability in rainfall results from the

dramatic topographic characteristics. At Kinlochewe at the South East end of Loch Maree, average rainfall was 2211 mm between 1961 and 1990, with an average of 11 gale days per annum. Daily temperature ranges in January and July are 0-6˚c and 10-16˚c respectively (Milner *et al.*, 2002). The geology of the area predominantly consists of Lewisian gneiss and Torridon sandstone, with much quartz at Beinn Eighe. The soils are shallow in areas of Lewisian gneiss, and generally have a peaty surface horizon (Milner *et al.*, 2002).

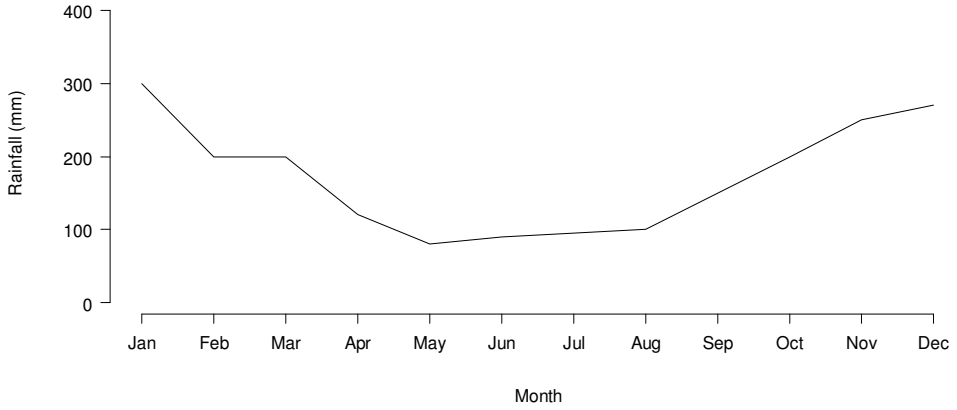


Figure 2. 1 The 23 year monthly average rainfall collected by SNH at Anancaun, Kinlochewe (NH 024632, 20 m) over the period 1975-78 and 1982-2000.



Figure 2. 2 Map indicating the location of the study region.



Figure 2. 3 Map indicating the locations of the study sites: Letterewe Estate and Beinn Eighe NNR in Wester Ross in the Scottish Highlands, UK, outlined by red boundaries.

2.1.1 The Letterewe oak woodland

The Atlantic oak woodland, characteristic of European western coastal fringes, on the shore of Loch Maree consists predominantly of oak *Quercus robur, Quercus robur* x *Q. rosacea* and *Quercus robur x Q. patrea* in varying proportions, with birch *Betula pendula* and *B. pubecens*, scattered rowan *Sorbus aucuparia,* ash *Fraxinus excelsior*, Juniper *Juniper communis* and holly *Ilex aquifolium.* Three woodland vegetation communities as defined in the National Vegetation Classification (NVC) are present: W11b *Q. petraea - B. pubescens - Oxalis acetosela, Blechnum spicant* sub-community; W17a *Q. patraea – B. pubescens – Dicranum majus, Isothecium myosuroides – Diplophylum albicans* sub-community; and W17c *Q. petraea – B. pubescens – Dicranum majus, Anthoxanthum odoratum – Agrostis capillaris* sub-community. The ground flora includes sweet vernal grass *Anthoxanthum odoratum,* sheep's fescue *Festuca ovina* and bilberry *Vaccinium myrtillus,* and a diverse flora of mosses, liverworts and lichens. Natural regeneration of oaks is prevented in part by seedling predation by deer, which has led to the instigation of the management strategy of erecting a series of grazing exclosures to facilitate regeneration. The shade formed by the closed canopy, in combination with caterpillars dropping from the canopy onto and predating seedlings, is the other main contributory factor in prevention of oak regeneration (Shaw, 1974). There is little or no understory outside the grazing exclosures. Exclosures were first established in 1961 and 1962 (dismantled in 2000), followed by further exclosures in later years. In this study, each grazing exclosure was paired with an adjacent un-fenced

(grazed) plot. Invertebrates were sampled in the epigeal and herb layers in both grazed and un-grazed treatment plots. Table 2.1 indicates grazing treatment, date of erection, the year(s) in which each plot were sampled, and the type of sampling carried out.



Figure 2. 4 Map indicating the location of the Letterewe oak woodland. The woodland is located along the north-east shore of Loch Maree, indicated by a red boundary.

2.1.2 Heather moorland invertebrate sampling

Six moorland plant communities as defined by the NVC are found at the study sites, three of which (M15, M17, H10) create a mosaic covering more than 68% of the land area of Letterewe Estate (Milner *et al.*, 2002). Here sampling concentrated on *Tricopherum cespitosum – Erica tetralix* (M15) wet heath which covers approximately 54% of the habitat at Letterewe and approximately 40% at Beinn Eighe. See Milner *et al.,* (2002) for a detailed description of Letterewe Estate. In 2007 I also attempted to sample Blanket Bog (M12), Summit Heath (U1/U11), and Dry Heath (H10) but in each case the shallow soil depth or very low vegetation height characteristic of the vegetation community prevented successful sweep netting and pitfall sampling and this was abandoned. 15 locations within M15 wet heath at Letterewe and 15 in M15 wet heath at Beinn Eighe were selected using randomised co-ordinates and sampled in 2007. Sweep net sampling (Southwood and Henderson, 2000) was used to sample invertebrates in wet heath at Letterewe and Beinn Eighe. Where sampling locations fell within 50 m of footpaths, fences or other topographical features that may have created a sampling bias, (for example proximity to fences may lead to local

increase in the number of avian predators attracted to perch sites (Hurlburt 1984)), they were discarded and replaced. Repeat visits were made to each site at four-weekly intervals from April to July 2008, after which time stalking activities prevented sampling at Letterewe. At each sample location, 3 x 100 m transects were swept along randomized angels of orientation. The operator made 100 approximately 1 m long quick strokes across the vegetation at each 1 m interval along the transect. This gave a total sample area per location of (3 x (100 m x 1 m) x 4 visits) = 1200 m^2. The contents of the net were emptied using an aspirator every 25 m to minimize loss of the catch, and were preserved in IMS until required. Sweeps were made in alternate directions to avoid repeat sampling of the vegetation, using a circular framed net with a diameter of 50cm, a white cloth bag, and a metal handle of 30cm. Sweep sampling collects biased samples of insects, however this is consistent between sampling locations, and has been shown to give comparable results to other sampling methods (Siemann et al., 1998). For Lepidoptera sampling from *Calluna vulgaris*, samples collected using a sweep net have been shown to correlate significantly with those from a combination of jarring and Berlease-Tullgren funnel extraction (Haysom and Coulson, 1998). While sweep sampling does not provide absolute estimates of insect populations (Southwood and Henderson, 2000) many researchers argue that a representative sample of the structure in invertebrate communities can be obtained (Janzen, 1973, Allen *et al*., 1973, Janzen and Schoener, 1968, Baines, 1994), and it is considered a current and valid method of invertebrate sampling (Crist et al., 2006). Sweep netting was preferred to the use of a D Vac vacuum sampler due the large study area, requirement to travel large distances between sample locations by foot due to the absence of roads, and the mountainous terrain. Adult invertebrates (except where indicated) were identified to one of the following taxonomic groups: Homoptera, Hemiptera, Coleoptera, Areneae, Diptera, Symphyta (larvae), Lepidoptera (larvae and adult). Other taxa were not present in samples in sufficient numbers to permit meaningful statistical analysis. Lepidoptera larvae were further identified to species after rearing on larval food plants using field guides (Skinner, 1984, Waring *et al.*, 2003) and expert assistant (personal communication: R. Leverton, 2008).

2.1.3 Woodland epigeal invertebrate sampling

Standard pitfall trapping (Woodcock, 2004) was used to sample epigeal invertebrates in grazed and un-grazed plots in the Letterewe oak woodland. In both 2007 and 2008 trap lines were operated consisting of 10 traps placed in a line, 10 m apart. The position of the first trap in the line was selected randomly, and its orientation positioned using randomly

generated compass degrees. Trap lines in adjacent sample plots were located a minimum of 100 m apart to eliminate edge effects and trap interference, and typically were considerably further apart. Traps were plastic cups of 75 mm diameter and 100 mm depth, each containing a 50% solution of ethylene glycol as a preservative to a depth of 60mm, and a small quantity of detergent to reduce surface tension and escapes. The rim of each trap was placed 1-7 mm below the soil surface, depending on soil depth, to eliminate the repulsion of invertebrates by protruding trap rims (Morrill *et al.* 1990; Good & Giller 1991). The efficiency with which different species of beetle are captured by pitfall traps varies between species, which necessitates a degree of caution when dealing with the data (Greenslade 1964). The presence of pitfall traps in the soil elicits different responses among different species, resulting in the capture of varying proportions of the beetle populations (Halsall and Wratten 1987). The inclusion in analyses of species captured in low abundance can result in errors, as they may be either tourists, very sedentary, or able to avoid capture. The analysis therefore deals only with the species captured most frequently, which combined make up approx 99% of the total number trapped. The individual locations of pitfall traps can affect their trapping efficiency (Luff, 1975).

The small-scale spatial difference in catch size between traps was avoided in this study by pooling catches from all traps at each site. A small number of traps were lost due to trampling by deer or other animals and were replaced at each monthly servicing interval. Losses due to trampling were not deemed sufficient to affect overall collecting efficiency. Each trap was fitted with a plastic cover to protect from flooding in heavy rain and prevent dilution of the preservative solution. The plastic covers also served to reduce accidental trapping of and predation by small mammals and birds. Covers can cause bias in pitfall trap catches (Joose 1965; Morrill 1975; Baars 1979), but the effect in this study was considered negligible due to the consistent use of the same material and colour for every trap. It has been suggested by some authors that the vegetation immediately surrounding pitfall traps can affect the rate of capture and therefore the overall numbers of invertebrates trapped (Greenslade 1964; Melbourne 1999). This may be due to an increase in the surface area available for animals to move on in structurally complex vegetation (Melbourne, 1999) which reduces the number of effective traps per unit of area. This effect is likely to be most pronounced for larger species, or those active on the surface of the ground (Greenslade, 1964). Throughout the growing season the structure will be fluid, and likely to change the rate of capture (Greenslade 1964; Melbourne 1999). It is therefore recommended that pitfall traps are not used to compare invertebrate populations in habitats with comparatively

different heterogeneous structures (Greenslade 1964; Maelfait & Baert 1975; Melbourne 1999). As this study necessitates just such a comparison, the vegetation immediately surrounding each trap was removed by cutting to ground level (Greenslade 1964; Penny 1966; Melbourne 1999). Different rates of activity between species dictate that they will have proportionally different rates of capture (Maelfait & Baert 1975; Curtis 1980) and that the number of each species caught is not an accurate measure of their true abundance. The concept of activity abundance hypothesises that the rate of capture will be a product of both abundance and activity (Tretzel 1954; Heydemann 1957; Thiele 1977). For these reasons trap catches can only be used to compare differences in population size between sites, and not to estimate their relative abundance (Baars 1979; Den Boer 1979). Taking these factors into consideration, data collected from pitfall traps are considered a valuable method for comparing populations between sites in this study. Traps were operated continually from May to October 2007, and April to September 2008, serviced at 4 weekly intervals. Trap catches were identified with the aid of taxonomic keys (Lindroth, 1974, Woodcock, 2006, Jessop, 1986) and expert assistance (personal communication: B.Woodcock, 2006, M. Barclay 2009).

2.1.4 Parasitoid and syrphid sampling

Flight intercept traps such as malaise traps are widely considered to be the most efficient method of collecting large, broad-spectrum samples of flying insects from a variety of habitats (Southwood and Henderson, 2000, Sutherland, 2006) and are commonly used for this purpose (Owen and Owen, 1974, Noyes, 1989b, Noyes, 1989a, Bartlett *et al.*, 1999, Sperber *et al.*, 2004, Fraser *et al.*, 2007, Sommaggio, 1999, Burgio and Sommaggio, 2007, Fraser *et al.*, 2008b). Samples can vary at small spatial scales (Fraser et al., 2007), therefore replication of traps within patches of habitat is recommended (Fraser *et al.*, 2008b). Therefore in each grazed or un-grazed plot two Malaise traps were installed to provide a measure of within plot variability, from April until August 2008. All traps used were of the design of Townes (*1972*) and were supplied by Marris House Nets (Marris House Nets, Bournemouth, UK). All traps were 1.8m high at the collecting head end, tapering to 1m high at the other end, and all were black in color. As these traps sample only in the field-herb layer, data were not collected for species predominantly found in the canopy. All traps were located on the south-west facing slope on which the woodland is located, to control for aspect, and all were orientated in the same direction to control for the effect of the plane of polarized light on trap catches. Traps were positioned at least 100 m apart both within and

between plots, and edge effects were controlled by locating traps at least 10 m, but often at least 100 m from plot edges. Data are not available on the effective sampling range of Malaise traps for hoverflies, which will potentially vary between species and habitat characteristics (Gittings et al., 2006). I however agree with the view of these authors that a 100 m radius between adjacent traps will render trap catches sufficiently independent from each other in terms of microhabitat feature effects. Traps were open continuously from April to September 2008 as a short sample duration is likely to produce biased community patterns (Fraser *et al.*, 2008b) and this length of sampling covers the main period of hoverfly and parasitoid flight activity (Gittings *et al.*, 2006, Fraser *et al.*, 2008a). Traps were serviced at four weekly intervals and all hoverflies caught were identified to species by R. K. Morris, and parasitoids to sub-family by D. L. J. Quicke. Large variation in trap catches between weeks necessitates that sampling regimes must span several consecutive weeks in order to capture temporal variability (Fraser et al., 2007).

Table 2. 1 Letterewe oak woodland sample plot locations, grazing status, size, date of erection, and sampling methods carried out for each year of study.

				Sampling			
				Malaise traps		Pitfall traps	
Location	Grazing	Area (ha)	Year erected	2007	2008	2007	2008
Ardlair	Grazed	N/A			*	*	*
	Un-grazed	2.5	1995		*	*	*
	Grazed (canopy gap)	N/A			*	*	*
Bad Burn	Grazed	N/A			*	*	*
	Un-grazed	14	2006		*	*	*
	Grazed (canopy gap)	N/A			*	*	*
Copperchy	Grazed	N/A			*	*	*
	Un-grazed	2.5	1995		*	*	*
Ruidh Dorcha	Grazed	N/A			*		*
	Un-grazed	10	2007		*		*
Kernsary	Un-grazed	2.5				*	
Regoilachy	Grazed	N/A			*	*	*
	Un-grazed	10	2006		*	*	*
Port an Aoil	Grazed	N/A				*	
Witches Point	Grazed	N/A			*	*	*
	Un-grazed	11	2006		*	*	*

Notes: Asterisks indicate use of sampling methods in each plot during each year of study. N/A indicates un-exclosed plots contiguous with the entire woodland.

2.1.5 Species richness and diversity indices

Two aspects of diversity were chosen for study, species richness and species evenness. Margalef's index was chosen to measure species richness, in preference simply to species number, as it compensates for sampling effects by dividing richness by the total number of individuals in the sample (Magurran, 2004). It is given by the following formula, where *S* is the number of species recorded, and *N* is the total number of individuals in the sample:

$$D_{Mg} = \frac{(S-1)}{\ln N}$$

Although strongly affected by sampling effort, it is an intuitively meaningful index, and this drawback is considered negligible in this study as sampling effort was identical across all comparisons. The Margalef index is simple to apply, and its use in conjunction with dominance or evenness weighted measured complementary, although caution is advised in its application to densities rather than absolute numbers of species (Gamito, 2010).

Simpson's index was preferred as a measure of species evenness, as its performance is well understood, has a low sensitivity to sample size, is widely used, does not require that species abundances follow a log series distribution, is dominance/evenness rather than richness biased, and has a good discriminate ability (Magurran, 2004). The index is calculated as:

$$D = \sum \left(\frac{n_i[n_i - 1]}{N[N-1]} \right)$$

where n_i = the number of individuals in the *i*th species, and N = the total number of individuals. Simpson's index is considered one of the most meaningful and robust diversity measures, and is expressed here as the compliment (1-D) as recommended by Lande (1996). It represents the probability of getting different species if two are selected at random from the sample, and the value of the index will increase at the community becomes more even. Lande *et al.,* (2000) found Simpson's index a better choice than species accumulation curves when ranking communities. These indices are used throughout this thesis.

2.1.6 Habitat survey: Heather moorland

At each of the wet heath sampling locations plant species were identified and visual estimates of percentage cover were made. Four 2 m x 2 m quadrats were sampled at randomly generated co-ordinates within each sampling location. Visual estimates of the percentage cover of non-gramminoid angiosperms and ferns were identified to species, as were gramminoids, with the exception of sedges (Cyperaceae) and rushes (Juncaceae) which were grouped as such. Lichens, bryophytes and lycopods were also grouped by class, and all were subsequently treated as pseudo-species. Total percentage cover could sum to more than 100 % due to overlapping vegetation. Vegetation height was quantified as a proxy for structural complexity and measured at 10 cm intervals at six randomly selected transects at each sampling location. The tallest plant structure at each interval was measured, and the species identified. Soil pH was measured using a calibrated electronic pH probe (accurate to 0.1 pH, Ph-03-1 meter, Xiamen Wondland Environmental Engineering Co. Ltd.). Three soil cores were taken at each sampling location, and the top 3 cm discarded to prevent distorted readings resulting from the accumulation of organic matter (Landeweert et al, 2002). 1.5 g from each sample was suspended in distilled water and the mean of the three samples taken as the pH of each site. Altitude was ascertained from Ordinance Survey Explorer maps and aspect quantified as either south-east or north-west facing.

2.1.7 Heather moorland explanatory variables

Listed here are the explanatory variables calculated for use in determining models of invertebrate responses to grazing pressure on Letterewe Estate and Beinn Eighe NNR.

Site - a two level factor, representing red deer grazing pressure implied by population density: 2.63 per 100 ha at Beinn Eighe, and 15 per 100 ha at Letterewe.

Vascular plant species richness - the Margalef index calculated from the mean relative abundances of vascular plants recorded at each sampling location. This measure has been shown to be an important predictor of insect diversity in grazed habitat (Kruess, 2002).

Vascular plant species diversity – the Simpson index calculated from the mean relative abundances of vascular plants recorded at each sampling location.

Vegetation height – the mean value of the maximum vegetation height at each sampling location.

Vegetation height variance – the variance of the vegetation height measurements taken at each sampling location.

Percentage cover of heather (*Calluna* and *Erica*) and *Molinia caerulea* – the mean percentage cover of visual estimates made at each sampling location. The encroachment of *Molinia caerulea* is considered one of the primary threats to moorland conservation, due to its inhibition of the development of dwarf shrub communities and its tendency to spread under the influence of overgrazing (Marrs et al., 2004). It is also a deterrent to foraging by meadow pipits *Anthus pratensis* (Vandenberghe et al., 2009). Heather declines under conditions of overgrazing by red deer (Grant et al., 1981), and is an important host of many moorland invertebrate species (Usher, 1992; Fielding, 1995; Hartley, 2003). *Calluna* and *Erica* cover are also reported to affect carabid assemblages (Ings, 1999).

Aspect – A two level factor based on whether each sampling location was either north-west or south-east facing, and considered biologically meaningful in terms of the incidence of solar radiation (Korner, 1999).

Altitude – the number of meters above sea level of each sampling location, determined using a hand-held GPS receiver.

Soil pH – the mean value of soil pH of the three soil cores taken at each sampling location.

Invertebrate abundance – the total number of invertebrates caught at each sampling location, shown to be an important predictor of spider abundance (Chen and Wise, 1999).

2.1.8 Habitat survey: oak woodland

A range of habitat variables were quantified in order to identify indicators of invertebrate abundance. Vegetation was sampled in July and August 2008 after the peak of the most productive growing period, both at the site of each malaise trap, and more widely across each sample plot, following the methods of *Fraser et al.,* (2007). Quadrats were of two scales: 20 x 20 m for canopy trees and the shrub layer, and 2 x 2 m for the field and herb layer. Malaise traps were located in the centre of a 20 x 20 m quadrat, within which five 2 m quadrats were surveyed. Two further 20 m quadrats were located in each sample plot at randomly generated co-ordinates, and five 2 m quadrats located at randomly generated co-ordinates surveyed within each, giving a total of four 20 x 20 m and twenty 2 x 2 m quadrats in each sample plot. All tree and woody shrub species over one meter in height were counted and identified to species in each 20 m quadrat. All herbs, grasses and woody shrubs less than one meter in height in the 20 m quadrats were identified to species. Fungi, mosses and liverworts, and lichens were not identified to species and were grouped as such and

subsequently treated as pseudo-species. Estimates of the percentage cover of each species/group were made visually for each 2 m quadrat. Total percentage cover could sum to more than 100 % due to overlapping vegetation. Canopy cover was estimated visually from the south-west corner of each 20 m quadrat using a gridded acetate held at arms length towards the canopy. The number of grid squares in which canopy was observed was divided by the total number in the grid. Species identification was aided using field guides (Blamey and Grey-Wilson, 2003, Hubbard, 1954) and expert assistance (personal communication: Prof. M. J. Crawley, 2007). Plant height and architectural diversity were quantified following the methods of Southwood *et al.,* (1979). A sampling pin 2 m in height was marked at 5 cm, 10 cm, and successive 20 cm intervals to a height of 1 m, and 25 cm intervals thereafter. In each height interval, the total number of plant touches in each category was recorded to provide a measure of plant height diversity, and the species of each of the plant structures touching the pin in each interval recorded and used to measure plant structural diversity. Samples were taken at five random co-ordinates using the pin, in each 2 m quadrat. The amount of leaf litter was quantified by visual estimation of cover in each 2 m quadrat.

2.1.9 Woodland habitat explanatory variables

Listed here are the explanatory variables calculated for use in determining models of invertebrate responses in the Letterewe oak woodland. Specific inclusion of variables in the analysis is detailed in the relevant chapters.

Year – potential year effects were investigated where sampling took place over multiple years by including year in statistical models.

Grazing – a two level factor grazed or un-grazed was determined to partition the effects of fencing to excluded grazing.

Plot size – The size of the fenced exclusion plots was recorded in ha to investigate effects of habitat patch size. The exclosures range in size from 2.5 to 14 Ha. Patches of habitat smaller than 2 ha may be incapable of supporting populations of invertebrates distinct from surrounding habitats (Levenson, 1981) and for this reason the dismantled exclosures at Port an Aoil and Allt Dearg, each being 0.5 ha, were not included in this study. Un-exclosed (grazed) plots were distinguished in the analysis by being arbitrarily assigned a size value of 100 ha. Plot size was subsequently found to be auto-correlated with grazing treatment and was therefore excluded from the analysis.

Exclusion duration – the age of the exclosure plots from date of construction was determined to test for effects of the length of grazing exclusion on invertebrates and the habitat. Un-exclosed (grazed) plots were assigned an exclusion duration of 0 years. Exclusion duration was subsequently found to be auto-correlated with grazing treatment and was therefore excluded from the analysis.

Deer density - Deer were occasionally seen inside woodland grazing exclosures as a result of damage to fences caused by tree fall, or after gaining access by swimming around the unfenced loch-side of some three-sided exclosures. Fence repair was prompt, and breeching events rare, however to provide an indication of deer use of both fenced and unfenced woodland plots, faecal pellet counts were carried out in July 2009. A standing crop strip transect count was preferred to an assessment of faecal accumulation rates as this method is suitable for large areas and most habitat types, and is not restricted by weather (other than snowfall). Only one site visit is required and labour requirement and equipment costs are low. The population estimate is for a period of at least 3-6 months. At deer densities below 30 per km^2 (15 per km^2 at Letterewe) the former is more practical in terms of effort and accuracy and is best suited to densities between 10-30 km^2. The method performs well as an estimate of population density or habitat use, and data analysis is relatively simple (Mayle, 1999). In each plot, 2000 m transects were selected at random, rejecting those that ran parallel to streams, fences, topographic or other features that may influence deer habitat use. Each transect formed a plot 2000 m x 1 m in size. Transects were walked along a bearing with the aid of a handheld GPS receiver. In each 10 m section, the number of pellet groups by species were recorded. A 1 m cane was used to measure the width of the transect, and pellet groups laying on the outer edge of the plot counted or rejected depending on the number of pellets falling inside or outside the search area. Groups exactly on the edge were alternately recorded or rejected. Density was calculated using the equation:

$$\text{Number of animals per ha} = \frac{\text{Number of pellet groups per ha}}{\text{Defecation rate (pellet groups per day) x mean decay time (days) for a pellet group}}$$

Defecation rate is taken to be 25 groups per day and Decay rate 365 days (Mayle et al 1999). Out of a total of 120 pellet groups counted, only two were roe deer, and no goat pellet groups were observed. All other groups were of red deer pellets, therefore roe pellet

groups were not included in the analysis and not considered a major grazing influence. Deer density was subsequently found to be auto-correlated with grazing treatment and was therefore excluded from the analysis.

Canopy cover – To investigate the effect of solar penetration through the canopy to the woodland floor, and the possibility of a cofounding effect due to exclosure placement in natural canopy gaps, canopy cover was estimated visually from the south-west corner of each 20 m quadrat using a gridded acetate held at arms length towards the canopy. The number of grid squares in which canopy was observed was divided by the total number in the grid and the percentage cover determined.

Vascular plant species richness (herb layer) – the Margalef index calculated from the relative abundances of vascular plants recorded in the herb layer, averaged over all quadrats to give a single value for each grazed or un-grazed plot. This measure has been shown to be an important predictor of insect diversity in grazed habitat (Kruess, 2002).

Vascular plant species diversity (herb layer) - the Simpson index calculated from the relative abundances of vascular plants recorded in the herb layer, averaged over all quadrats to give a single value for each grazed or un-grazed plot.

Herb species diversity (herb layer) - the Simpson index calculated from the relative abundances of herbaceous plants recorded in the herb layer, averaged over all quadrats to give a single value for each grazed or un-grazed plot.

Tree species richness – the Margalef index calculated from direct counts of the relative abundance of all individuals located in all of the four 20 m quadrats sampled in each grazed or un-grazed plot.

Tree species diversity – the Simpson index calculated from direct counts of the relative abundance of all individuals located in all of the four 20 m quadrats sampled in each grazed or un-grazed plot.

Tree/shrub species richness – the Margalef index calculated from the relative abundances of tree species recorded, averaged over all quadrats to give s single value for each grazed or un-grazed plot, and has been shown to be an important influence on parasitoid communities in cacao agroforestry (Sperber et al., 2004).

Tree/shrub species diversity - the Simpson index calculated from the relative abundances of tree and shrub species recorded in the herb layer, averaged over all quadrats to give a single value for each grazed or un-grazed plot.

Flowering plant species richness – the Margalef index calculated from the relative abundances of flowering plant species recorded in the herb layer, averaged over all quadrats

to give a single value for each grazed or un-grazed plot. Flowering plant species richness has been shown to increase the frequency and diversity of pollinator visits (Haslett, 1989, Ebeling *et al.*, 2008).

Flowering plant species diversity - the Simpson index calculated from the relative abundances of flowering plant species recorded in the herb layer, averaged over all quadrats to give a single value for each grazed or un-grazed plot.

Flowering plant cover – the percentage cover of flowering plants calculated from visual estimates of vegetation species cover, averaged over all quadrats to give a single value for each grazed or un-grazed plot

Grass-herb species ratio – the ratio of the relative abundance of grass to herb species recorded in the herb layer, which has been shown to influence insect diversity in grazed habitat (Kruess, 2002).

NVC – to determine whether the plant community was important in determining invertebrate responses, the NVC plant community was included as a three level factor.

Bracken – *Pteridium aquilinum* is prolific and abundant, particularly in the highlands, and often considered an invasive competitively dominant species detrimental to various habitat types, despite hosting between 27 – 40 invertebrate species (Marrs and Watt, 2006). To test for any effect of bracken abundance within the woodland, and any confounding effect with its proliferation in fenced, sunlight canopy gaps, the visual estimate of percentage cover was included in models of invertebrate response.

Leaf litter – the percentage cover of leaf litter on the woodland floor, averaged over all quadrats for each grazed or un-grazed plot.

Moss – percentage cover of bryophytes on the woodland floor, averaged over all quadrats for each grazed or un-grazed plot, shown to be an important predictor of carabid abundance in native Scottish forest (Ings, 1999).

Vegetation height – the maximum height of the vegetation taken from and averaged over the 20 sampling pin measurements for each grazed or un-grazed plot.

Vegetation height diversity - the log series diversity index α was used to estimate plant height diversity from the sampling pin data, after Southwood *et al.,* (1979) who found it an important predictor of insect diversity in successional habitat, and a good proxy for structural complexity.

Plant species structural diversity - the log series diversity index α was used to approximate a measure of the structural complexity of the vegetation based on the variation in structure attributable to different plant species, and calculated from the sampling pin data.

The count of the number of touches of each species constitutes a precise estimate of the distribution of the structures of different plant species in the vertical plane, and the index an estimate of the diversity of this structural complexity.

Grass/herb/shrub alpha – a measure of the structural complexity of the vegetation using the log series diversity index α, attributable to the range of morphologies distinct to grasses, herbs and shrubs (Lawton and Schroder, 1977). The continuum from monocotyledons, through herbs and shrubs to trees, exhibits increasing size and architectural complexity, and an associated increased in the diversity of associated insects (Lawton, 1983, Strong *et al.*, 1984).

Chapter 3

Invertebrates and red deer in heather moorland

Abstract

Concern over the detrimental impacts of grazing due to increasing deer numbers has lead to conflicting objectives between conservation and deer managers, the former often seeking to reduce deer numbers and the later to maintain or increase them. Despite significant variation in deer numbers and vegetation, the abundance of moorland invertebrates between two moorland estates was predicted variously by a range of habitat variables, but the anticipated effect red deer grazing pressure was only important in determining two aspects of the Lepidoptera assemblage. This study provides little evidence for negative impacts of grazing on the more heavily grazed Letterewe estate, suggesting that at current numbers, the deer population is not a cause for concern over invertebrate biodiversity. This work highlights the need for science to inform land management policy that must often seek to balance conservation objectives with economic interests. It also supports the notion that a red deer herd of a size consistent with viable stalking interests can be integral to the maintenance of both heather moorland biodiversity and the natural heritage.

3.1 Introduction

Upland heather moorland is a habitat of international conservation importance with a large proportion of the global resource occurring in the UK, particularly the highland region of Scotland (Gardner *et al.*, 1997). This habitat however has undergone dramatic declines in recent decades, with the area of upland heather moorland in Scotland estimated to have decreased by 18% between the 1940's and 1970's (Littlewood, 2006a). Because of its global rarity and the threats posed to it, upland heather moorland has been recognised as a Biodiversity Action Plan (BAP) priority habitat, and the 13 plant communities included

within this habitat type are protected under the EU habitats directive (Thompson et al., 1995). The main threats to heather moorland include afforestation, agricultural reclamation, grazing pressure, invasion by bracken *Pteridium aquilinum,* nitrate enrichment from pollution (Terry, Ashmore et al. 2004), and climate change (Holden et al., 2007).

Heather moorland is a very distinctive habitat, derived from woodland or scrubland, and characterised by the common heather *Calluna vulgaris* plant (Thompson et al., 1995). Two main communities are recognised in the NVC, dryer *Calluna* heath (H10 *Calluna vulgaris – Erica cinerea* dry heath), and wetter heather dominated blanket bog (M15 *Tricopherum cespitosum – Erica tetralix* wet heath), at opposing ends of a climatic gradient (Usher and Thompson, 1993, Rodwell, 1991). Climatic conditions tend to be wet with > 100 cm rainfall pa, and occurrence is generally on shallow acidic peaty soils (pH < 6.5) (Thompson et al., 1995). Although in many parts of Scotland heather moorland persists naturally (Gardner, 1991), paleopalynological studies reveal that heathland vegetation composition does not correlate with the prevailing climatic conditions and thus it is considered to be a landscape of anthropogenic origin (Dodgshon and Olsson, 2006). The successional stage of the vegetation is maintained through activities such as livestock grazing, peat cutting and burning. Historically these activities were largely carried out for sheep grazing, while now it is largely for grouse and red deer sporting interests. Despite its anthropogenic origins the habitat is of considerable value with regards to biodiversity conservation, landscape, aesthetic and tourism benefits (Thompson et al., 1995), and consequently the loss of heather dominated ecosystems to grassland is generally considered undesirable (Littlewood, 2006a).

The flora while rich in dwarf shrubs is relatively impoverished, but supports a rich faunal assemblage. Moorlands support a significant proportion of UK invertebrate species (Gardner *et al.*, 1997) including a diverse fauna of epigeal invertebrates (Usher and Thompson, 1993), although in some areas this can be impoverished with respect to certain taxa such as Coleoptera (Milner *et al.*, 2002). In contrast *Calluna-Vaccinium* heaths can be particularly rich in Lepidoptera, whose richness declines with altitude (Haysom and Coulson, 1998). The invertebrate community in turn provides the main source of food for a very distinct avian assemblage comprising between 40 and 50 species, eight of which are listed under the EC Birds Directive (Buchanan et al., 2006) and a further 28 species that are of conservation concern in the UK (Thompson et al., 1995). Moorland birds depend predominantly on an invertebrate diet, consisting of very few taxa, including Arachnida, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Oligochaeta, of which the

beetles and flies are most important (Buchanan et al., 2006). Although data on moorland birds is scarce, sheep grazing is thought to impact their abundance though reduction of preferred vegetation types, changes to food supplies and alteration of predation pressure (Fuller and Gough, 1999). Moorland vertebrates other than birds include the Mountain hare *Lepus timidus,* field vole *Microtus agrestis,* wood mouse *Apodemus sylvaticus,* common shrew *Sorex araneus,* fox *Vulpes vulpes,* badger *Meles meles,* pine marten *Martes martes,* weasel *Mustelia nivalis,* stoat *Mustela erminea,* pipistrelle bat *Pipistrellus pipistrellus,* red deer *Cervus elaphus*, sika deer *Cervus nippon*, common lizard *Lacerta vivipara,* slow worm *Anguis fragilis,* grass snake *Natrix natrix,* adder *Vipera berus,* common frog *Rana temporaria,* common toad *Bufo bufo,* and palmated newt *Titurus helveticus.*

3.1.1 Grazing on heather moorland

Studies of grazing impacts in heather moorland have focused primarily on the impacts of domestic livestock (Bokdam and Gleichman, 2000, Hartley and Mitchell, 2005, Bell et al., 2001, Bullock and Pakeman, 1997, Cole et al., 2006, Gardner et al., 1997, Hartley, 2003, Hope et al., 1996, McFerran et al., 1994, Grant and Armstrong, 1993, Hanley et al., 2008) with a strong bias towards grazing impacts on plant communities. In contrast, relatively few have examined the impacts of red deer on heather moorland plant communities (Milner et al., 2002, Hewson, 1976, Moss, 1981, Grant et al., 1981, Virtanen et al., 2002) and of red deer on invertebrates in pinewoods (Baines et al., 1994). Furthermore, to my knowledge there are no studies that have specifically investigated the impacts of grazing by red deer on invertebrates in heather moorland, but see section 3.3 for details of studies regarding the impacts of domestic livestock. Grazing impacts biodiversity and in particular invertebrates in various ways. For example, higher grazing densities that create lower sward heights may result in increased botanical diversity as a result removal of competitively dominant species (Olff and Ritchie, 1998). This may in turn affect invertebrates by altering the range of available niches. A review of the mechanisms of grazing impact can be found in Chapter One.

The relationships between red deer grazing and the impacts on heather moorland communities are likely to be complex. Red deer grazing is selective, with feeding preferences varying according to vegetation height (Moss, 1981), the age of heather, and according to the season (Hewson, 1976, Welch, 1984a). Younger heather is less able to withstand grazing (Grant et al., 1981) and is neglected as a source of food by red deer (Moss, 1981). Grant *et al.,* (1981) also point out that red deer select a mixed heather-grass

diet throughout the year with grasses the dominant component in the summer, due in part to the high quality food requirements of lactating females (Landete-Castillejos et al., 2003). Protection from grazing increases heather production and alters chemical composition, and red deer show preference for heather growing in nitrogen rich areas (Moss, 1981, Milner et al., 2002). Heavy grazing can reduce heather cover (Welch, 1984b) and facilitate transition to monocotyledonous communities of unpalatable graminoids such as *Nardus stricta*, *Juncus squarrosus* and *Molinia caerulea* (Welch, 1986, Littlewood, 2006b), while light grazing favours ericoids and lichens (Welch, 1984c). Welch also found that only two moorland plants, *Nardus stricta* and *Vaccinium myrtillus,* preferred intermediate levels of grazing, and that the response of bryophytes was variable. Decline in heather cover results in increases in graminoids and forbs, and declines in ericoids and lichens (Welch and Scott, 1995). In a study conducted at Letterewe, a visible effect of red deer grazing on vegetation biomass was only evident in 18 out of 244 harvests from inside and outside of grazing exclosures (Milner et al., 2002). Botanical diversity at Letterewe was not unusually low due to deer grazing (391 species), and was close to the average figures for the same NVC communities nationwide. Green heather productivity estimates were consistent with the expected figures for the geographical region, and heather condition was generally good. Flower density of both herbs and graminoids however, was significantly reduced outside of grazing exclosures. Grazing by red deer is considered a potential driver of plant diversity (Milner et al., 2002, Virtanen et al., 2002). Virtanen *et al.,* (2002) found that long term deer exclusion was associated with a reduction in species richness in productive, and a negligible effect in unproductive plant communities.

3.1.2 Grazing effects on moorland invertebrates

Grazing effects on invertebrates in heather moorland show varied trends. Many studies show that more intense grazing pressure leads to a reduction in abundance (Dennis 2001; Dennis 2004) biomass (Dennis et al., 2008) and species richness (Dennis *et al.*, 2008, Kruess, 2002). In contrast, some studies have found evidence that grazing can be beneficial to invertebrate abundance and diversity (Gonzalez-Megias, 2004). A pattern evident from previous studies is that the response of invertebrates to grazing may vary in both magnitude and direction depending on the taxonomic group and guild being studied (Littlewood, 2008, Gibson, 1992b). For instance, monophagous species may persist only where grazing suppresses competitively dominant species that interact with the food plant (Poyry et al., 2004) and phytophagous invertebrate communities may contain more generalist species

where grazing is less intense (Littlewood, 2006b). Loss of *Calluna* from moorland and the associated transition to graminoid dominated communities results in increased richness of plants and phytophagous Hemiptera species (Littlewood, 2006b). Other guilds may respond differently, for instance carabids are sensitive to the character and extent of the *Calluna* stand (Gardner *et al.*, 1997). Restoration of moorland can result in a return of the phytophagous invertebrates associated with *Calluna* (Littlewood, 2006a). Plant community composition, vegetation height and grazing treatment were the strongest predictors of spider, harvestman and pseudoscorpion abundance in a *Nardus strica* grassland (Dennis *et al.*, 1997), while epigeal spiders were unaffected. More spider webs were found in taller un-grazed swards. Significant grazing effects on carabids were correlated with vegetation height, stocking density, and botanical diversity in grazing treatments. Large web spinning spiders have been shown to be a particularly sensitive group to grazing due to their requirement for stable vegetation structures, with heavily grazed treatments containing a large proportion of a group of Linyphiidae characteristic of disturbed land (Gibson, 1992a). Aspects of the vegetation architecture were the strongest predictors of spider assemblies, in contrast to other invertebrate groups that were more strongly influenced by botanical diversity. Taller un-grazed swards also support more carabids than grazed swards (Dennis, 2004). Some invertebrate groups then respond to changes in architecture, while others are more dependent on botanical diversity. Disentangling the effects of these factors is vital to our understanding the response of invertebrate communities to the vegetation changes associated with grazing (Gibson, 1992a).

The practice on some stalking estates of supplementary winter feeding can exacerbate the impacts of grazing by maintaining an artificially high deer population through the summer, which counteracts the regulatory effect of natural winter mortality. In moorland agricultural systems, intense grazing pressure is exerted by large numbers of sheep moved onto the hill during the summer months. Heavy sheep grazing can have significant impacts on biomass, height and shoot structure of heather with associated impacts of heather height on carabid communities (Gardner *et al.*, 1997). Gardner *et al.,* found a transition from beetles associated with shady taller vegetation to those associated with open ground, between low and high intensity grazed sites, and a reduction in species richness in intensely grazed sites. Sheep and cattle grazing can cause a reduced abundance of spiders, bugs and beetles (Dennis *et al.*, 2008) and reduced abundance and richness of moths (Littlewood, 2008).

In other ecosystems there is evidence of positive effects of grazing on invertebrate communities. In the Sierra Nevada National Park, ungulate grazing exclosures had higher abundances of invertebrates than grazed plots, and although an effect on species composition was observed, diversity did not decrease (Gonzalez-Megias, 2004). This effect was also correlated with reduced botanical diversity and structural complexity, which is contrary to the traditional view. In this study, grazing produced open ground with suitable nest sites and microclimatic conditions for ants, however these conditions would be unsuitable for other invertebrate groups that may exhibit a different response. This indicates the importance of considering the ecological traits of the invertebrate groups considered when investigating grazing impacts.

The continuum from monocotyledons, through herbs and bushes to trees, is accompanied by increasing size and architectural complexity, and this in turn is associated with an increase in the diversity of associated insects (Lawton, 1983, Strong *et al.*, 1984, Southwood *et al.*, 1979). Trees and shrubs may support more than 10 times the number of macro-Lepidoptera than grasses (Tahvanainen, 1982). Taller vegetation is expected to support more diverse invertebrate communities, by offering both greater apparency to prospecting invertebrates and greater opportunities for competition avoidance, niche availability and resource partitioning. In some instances the effects of vegetation structure are relatively direct. An uneven distribution of noctuid larvae on spurge laurel *Daphne laureola* was positively correlated with leaf whorl abundance and negatively with basal stem diameter, and attributed to discriminatory oviposition behaviour by females responding to variation in these traits (Alonso and Herrera, 1996). In addition to such direct effects of host plant architecture on invertebrate populations, vegetation structure can also act indirectly via its impacts on natural enemies. In a study of ladybird predation on pea aphids, structural variation between two closely related lines of pea led to marked difference in predation rates between plants with and without leaves (Kareiva and Sahakian, 1990). The numerous ways through which plant architecture may influence insect abundance make predicting the specific effects of changes in vegetation complexity challenging (Godin, 1999, Hanan, 2002). For many shrubby species such as heathers and bog myrtle there are clear differences in the availability of resources offered by plants along an age gradient. *Calluna* for example has a thick layer of litter used by overwintering Lepidoptera pupae, which is not available under younger pioneer plants (Haysom and Coulson, 1998).

Invertebrates of moorlands are comparatively more species rich than plants or vertebrates in these habitats (Usher and Thompson, 1993). This is particularly true with

respect to predatory groups such as carabid beetles and spiders (Usher, 1992) and invertebrates are vital functional components of these ecosystems (Coulson, 1988). Changes in moorland vegetation under different management regimes are well understood, whereas invertebrate responses are understudied. This knowledge is required in the formation of management plans, of which the primary focus is currently on vegetation characteristics. This approach means that management objectives do not always take account of wider aspects of biodiversity. The research described here uses heather moorland under two extremes of grazing pressure, to investigate the effects of grazing by red deer on invertebrate responses. Various invertebrate groups were used in order to investigate guild responses to changes caused by grazing. The Hemiptera are primarily a sap-feeding family making them a useful group with which to study responses to vegetation change (Littlewood, 2006b). They have previously been shown to respond to botanical composition, structure, host plant quality, soil characteristics, and altitude (Gimingham, 1985b, Littlewood, 2006b). Lepidoptera are a phytophagous group also sensitive to changes in vegetation composition (Littlewood, 2006a) associated with grazing (Littlewood, 2008). They are an important component of the diet of moorland birds (Evans *et al.*, 2006b, Buchanan, 2006) and provide key ecosystem services in the form of nutrient cycling (Littlewood, 2008). Long term population trends provide considerable cause for concern (The State of Britain's Moths, Butterfly Conservation Report 2007). The Curculionidae are primarily a group of foliar phytophagous Coleoptera that may respond to changes in botanical composition (Morris, 2002), while spiders are exclusively carnivorous and have a wide range of foraging behaviours. This means that they require specific plant and soil structure characteristics, and can be expected to show relatively little response to botanical composition (Gibson, 1992a). They should therefore be a good taxonomic group with which to investigate invertebrate responses to changes in vegetation structure caused by grazing, and may also respond to prey availability (Dennis et al., 2008). The Diptera are a diverse taxonomic group and the Tipulidae in particular are an important source of food for moorland birds (Buchanan et al., 2006). They exhibit a wide range of feeding strategies and include leaf miners, blood suckers, dung, carrion, mucous, nectar and sap feeders, and predators. They may therefore be expected to respond to a range of habitat alterations associated with by grazing. Hymenoptera contain the largely phytophagous Symphyta, pollen and nectar feeding Apoidea, and Vespoidia which feed on a wide range of food sources including other invertebrates and plants.

3.2 Aims

Here the hypothesis that grazing by red deer has the potential to alter habitat conditions such as vegetation architecture and species diversity, in turn affecting the availability of resources to moorland invertebrates, is tested. The aims of this chapter are:

- To compare invertebrate assemblages under two levels of red deer grazing pressure, mediated by contrasting management strategies.
- To assess which of a range of potential habitat variables best explain the variation in invertebrate responses.
- To make recommendations for the management of red deer on Letterewe estate that are consistent with the maintenance of biodiversity.

The hypotheses that moorland invertebrate assemblages do not vary under extremes of grazing pressure and are not associated with habitat variables were tested, on two moorland estates, Letterewe and Beinn Eighe, details of which can be found in Chapter Two. By identifying the primary components that determine moorland invertebrate diversity, it will be possible to asses more effectively the consequences of management practises and grazing policy for biodiversity in red deer habitats.

3.3 Methods

For a description of the general methods used see Chapter Two.

3.1.3 Statistical analysis

Statistical analyses were performed using the software R 2.10.1 for Windows (R Development Core Team, 2010) following established techniques (Sokal and Rohlf, 1995, Crawley, 2007). Generalized Linear Models were used to test the null hypotheses that invertebrate responses showed no response to grazing pressure between the two estates. Analysis of abundance data were performed using GLM's with a Poisson error structure, or quasipoisson where there was over dispersion in the response, as was typical. Species richness and diversity measures were analysed using GLM's with a normal error structure. The distribution of non-count data was examined graphically and either log or square root transformed as appropriate to improve normality in the residuals. Tree models were used to obtain a preliminary ranking of the importance of the explanatory variables in order to

distinguish those that best explained the variation in the data, and these were used these for initial parameterisation of GLM's. Initially all explanatory variables and quadratic terms for continuous variables were fitted individually to test for significance, and graphical inspection used to look for curvature in the response. A top down model of all explanatory

Table 3. 1 Explanatory variables used in the analysis of heather moorland invertebrate responses to grazing pressure at Letterewe and Beinn Eighe.

Variable	Invertebrate response								
	Homoptera	Heteroptera	Coleoptera	Arenaea	Diptera	Lepidoptera			
						Larvae	Broom moth	Richness	Diversity
Site	*	*	*	*	*	*	*	*	*
Calluna vulgaris	*	*	*	*	*	*	*	*	*
Erica sp.	*	*	*	*	*	*	*	*	*
Vascular plant species richness	*	*	*	*	*	*	*	*	*
Vascular plant species diversity	*	*	*	*	*	*	*	*	*
Vegetation height	*	*	*	*	*	*	*	*	*
Vegetation height variance	*	*	*	*	*	*	*	*	*
Aspect	*	*	*	*	*	*	*	*	*
Altitude	*	*	*	*	*	*	*	*	*
Soil pH	*	*	*	*	*	*	*	*	*
Invertebrate abundance				*					

Notes: See Chapter Two for detailed descriptions of explanatory variables.

terms was then fitted to the data including interaction terms, with inclusion of interactions limited to two-way terms, as far as replication in the data would allow. The least significant, highest order interactions were deleted sequentially until all remaining terms were significant at $P < 0.05$ to produce the minimal adequate model (MAM). All MAM's were checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity and the ordered residuals against the normal scores to look for evidence of non-normality of errors. Where heteroscedasticity occurred the response variable was transformed and the model re-evaluated. Candidate models were compared using ANOVA to justify retaining or excluding variables, or Akaike's information criterion

(AIC) used to compare model fit for models with a normal or Poisson error structure. Where the ANOVA indicated no significant difference between the models ($P > 0.05$) the model with the highest degrees of freedom was retained. Where a significant difference occurred the model with the lowest residual deviance was retained. To plot graphical representations of significant interactions, linear models were used to determine the threshold value above and below which splitting the variable the difference between models was most significant. Lines were fitted using the predict function in R which uses information from the fitted model to produce a smooth function with which to plot the model from the data.

3.4 Results

A total of 10,506 individuals belonging to nine invertebrate groups were collected across 30 locations, from wet heath on two estates under either high (Letterewe) or low (Beinn Eighe) grazing pressure from red deer.

3.4.1 Grazing effects

Of 9 invertebrate responses examined, Homoptera were more abundant at Letterewe than at Beinn Eighe, while Lepidoptera species richness and diversity were significantly higher at Beinn Eighe than at Letterewe (see table 3.2 and figure 3.1). There were no significant differences in abundance between the two estates for Heteroptera, Diptera, Areneae, and Lepidoptera larva (see table 3.2 and figure 3.1). In many instances the abundance of invertebrate groups did not differ between estates despite the presence of outlying data points. Outliers were examined to check for possible inaccuracies or factors peculiar to the sampling location, and where nothing remarkable was identified these data points were retained in the analysis, as was typical.

3.4.2 Effects of other habitat variables

Other than estate, the only significant predictor of Homoptera abundance was altitude, which was associated with a steep negative linear response (figure 3.3a). Heteroptera abundance was significantly higher at north-west than south-east facing sampling locations (figure 3.3b), and was influenced by the interaction between vegetation height and vegetation height variance (figure 3.4). Low vegetation height caused an exponential decline in Heteroptera abundance in response to vegetation height variance, while taller vegetation was associated with a shallower negative linear decline. Coleoptera abundance showed significant correlations with soil pH (figure 3.5a), vegetation height variance (figure 3.5b), *Erica* spp. percentage cover (figure 3.5c), and to interactions between estate and altitude (figure 3.6), and altitude and vascular plant species diversity (figure 3.7). Soil pH and *Erica* spp. percentage cover caused significant negative linear declines, while the significant positive linear relationship between Coleoptera abundance and vegetation height variance maybe somewhat influenced by a single data point, however examination for idiosyncrasy justified its retention in the model. At Beinn Eighe the relationship between Coleoptera abundance and altitude was slightly negatively linear, and at Letterewe slightly positively linear.

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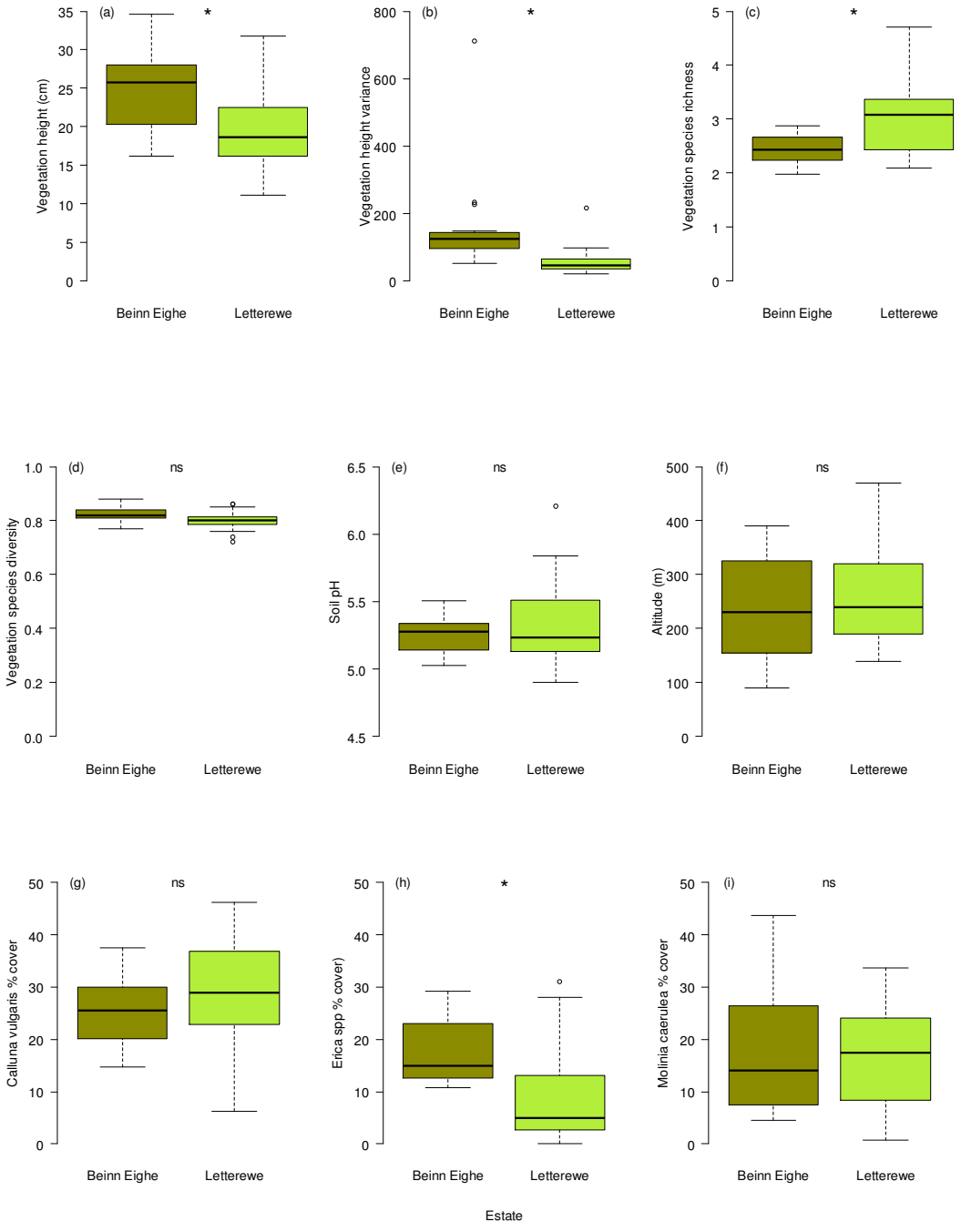


Figure 3. 1 Boxplots illustrating differences in vegetation, soil and altitude characteristics between Beinn Eighe and Letterewe. (a) Vegetation height (b) Vegetation height variance, (c) Vegetation species richness, (d) Vegetation species diversity, (e) Soil pH, (f) Altitude, (g) *Calluna vulgaris* % cover, (h) *Erica* spp % cover (i) *Molinia caerulea* % cover. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002). Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***, non-significant differences are indicated by 'ns', means compared using *t* tests, n=30, for statistics see table 3.2.

Table 3. 2 Differences in vegetation characteristics between Beinn Eighe and Letterewe. t value: model t statistic. *P*: model *P* value. df: degrees of freedom.

	Mean					
Variable	Grazed	Un-grazed	*t*	Df	*P*	
Vegetation height	24.751	19.747	2.619	28	0.014	*
Vegetation height variance	165.821	61.916	2.418	28	0.022	*
Vegetation species richness	2.441	3.034	-2.758	28	0.01	*
Vegetation species diversity	0.823	0.799	1.834	28	0.077	ns
Soil pH	5.252	5.330	-0.769	28	0.449	ns
Altitude	237.333	266.000	-0.793	28	0.435	ns
Calluna vulgaris % cover	25.783	29.083	-0.940	28	0.355	ns
Erica spp % cover	18.067	9.517	2.727	28	0.011	*
Molinia carulea % cover	17.833	17.067	0.184	28	0.855	ns

Notes: Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***. Non-significant differences are indicated by 'ns', n=30.

Table 3. 3 Effect sizes and their standard errors of invertebrate group abundance. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

	Estimate	SE	*t* value	*P*		Res. Dev.	df
Homoptera							
Estate (Beinn Eighe)	5.496	0.544	10.095	< 0.001	***	3192.9	27
Altitude	-0.005	0.002	-2.079	0.047	*		
Estate (Letterewe)	1.044	0.410	2.547	0.017	*		
Heteroptera							
Intercept	6.345	0.898	7.066	< 0.001	***	216.86	25
Vegetation height variance	-0.053	0.014	-3.810	0.001	***		
Vegetation height	-0.111	0.035	-3.202	0.004	**		
Aspect (SE)	-0.600	0.265	-2.266	0.032	*		
Vegetation height variance : vegetation height	0.002	0.001	3.738	0.001	***		
Coleoptera							
Estate (Beinn Eighe)	11.788	6.741	1.749	0.095	.	43.335	21
Soil pH	-0.891	0.373	-2.391	0.026	*		
Vegetation height variance	0.002	0.001	3.423	0.003	**		
Estate (Letterewe)	-0.799	0.551	-1.450	0.162			
Erica sp. percentage cover	-0.035	0.016	-2.177	0.041	*		
Vascular plant species diversity	-5.699	7.678	-0.742	0.466			
Altitude	-0.054	0.024	-2.276	0.033	*		
Estate : altitude	0.005	0.002	2.183	0.041	*		
Altitude : vascular plant species diversity	0.065	0.029	2.258	0.035	*		
Diptera							
Intercept	166.650	52.624	3.167	0.004	**	775.650	25
Vascular plant species diversity	-193.426	63.734	-3.035	0.006	**		
Aspect	0.541	0.212	2.554	0.017	*		
Soil pH	-29.643	9.930	-2.985	0.006	**		
Vascular plant species diversity : soil pH	35.278	12.006	2.938	0.007	**		
Symphyta							
Intercept	102.383	16.979	6.030	< 0.001	***	73.958	24
Soil pH	-16.010	2.792	-5.735	< 0.001	***		
Vascular plant species diversity	-18.987	4.581	-4.145	< 0.001	***		
Vegetation height	-2.967	0.542	-5.470	< 0.001	***		
Altitude	-0.004	0.002	-2.322	0.029	*		
Soil pH : Vegetation height	0.563	0.105	5.382	< 0.001	***		
Areneae							
Estate (Beinn Eighe)	4.304	1.226	3.510	0.002	**	132.320	23
Invertebrate abundance	0.006	0.002	3.365	0.003	**		
Estate (Letterewe)	-3.953	1.426	-2.772	0.011	*		
Vascular plant species richness	-1.178	0.525	-2.243	0.035	*		
Altitude	0.005	0.003	1.750	0.093	.		
Site : vascular plant species richness	1.530	0.561	2.728	0.012	*		
Invertebrate abundance : altitude	0.000	0.000	-3.150	0.004	**		

Notes: Minimal adequate models for (a) Homoptera abundance as a function of estate and altitude. Explanatory variables excluded during model simplification included soil pH : altitude P = 0.588, altitude : estate P = 0.344, soil pH : estate P = 0.358, soil pH P = 0.428, estate : Calluna vulgaris % cover P = 0.554, altitude : Calluna vulgaris % cover P = 0.520, estate : Erica spp. % cover P = 0.943, altitude : Erica spp. % cover P = 0.254, Erica spp. % cover P = 0.935, estate : vascular plant species diversity P = 0.552, altitude : vascular plant species diversity P = 0.306, estate : vascular plant species richness P = 0.980, altitude : vascular plant species richness P = 0.623, altitude : vegetation height P = 0.731, estate : vegetation height P = 0.340, vegetation height P = 0.525, altitude : vegetation height variance P = 0.874, estate : vegetation height variance P = 0.540, estate : Molinia caerulea % cover P = 0.665, altitude : Molinia caerulea P = 0.533, altitude : aspect P = 0.821, estate : aspect P = 0.693, aspect P = 0.261. (b) Heteroptera abundance as a function of aspect, and the interaction between Vegetation height variance and vegetation height, (c) Coleoptera abundance as a function of soil pH, vegetation height variance, *Erica* spp. percentage cover, and the interactions between estate and altitude, altitude and vascular plant species diversity, (d) Diptera abundance as a function of aspect, and the interaction between vascular plant species diversity and soil pH, (e) Symphyta abundance as a function of vascular plant species diversity, altitude, and the interaction between soil pH and vegetation height, (f) Areneae abundance as a function of the interactions between estate and vascular plant species richness, and invertebrate abundance and altitude. Model simplification for all models follows the same protocol as (a). See Chapter Two for a full explanation of each of the explanatory variables. Models of abundance data are generalized linear models with a quasipoisson error structure. Asterisks indicate the level of significance: *P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***.*

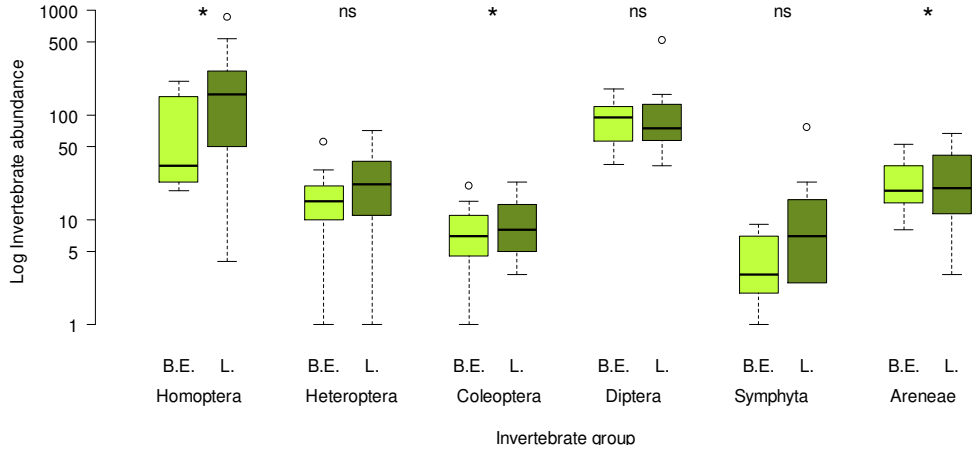


Figure 3. 2 Boxplot illustrating the abundance of invertebrate groups sampled at Beinn Eighe and Letterewe. B.E. = Beinn Eighe (Low grazing pressure = 2-3 deer per 100 ha), L. = Letterewe (high grazing pressure = 15 deer per 100 ha). Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002). Significant differences in abundance were detected in the generalised linear models for Homoptera, Coleoptera and Areneae, (see table 3.2 for statistics), no difference in abundance was detected in the generalised linear models for Heteroptera (Estimate = 0.039, SE = 0.310, t value = 0.126, *P* = 0.901), Diptera (Estimate = 0.208, SE = 0.331, t value = 0.631, P = 0.534), and Symphyta (Estimate = 0.476, SE = 0.695, t value = 0.685, *P* = 0.5). Non-significant estimates, SE's, *t* and *P* values are the deletion values taken from the relevant model simplification. Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***, ns = not significant, n = 30.

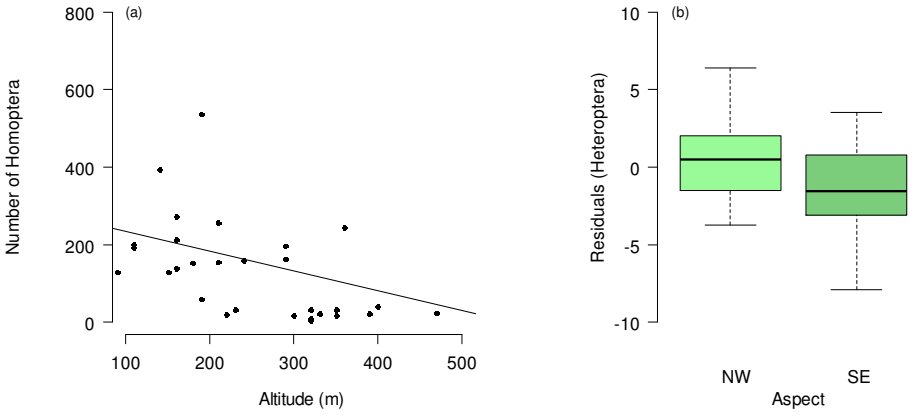


Figure 3. 3 The response of (a) Homoptera abundance to altitude, and (b) Heteroptera abundance to aspect. (a) A significant effect of altitude was detected in the generalised linear model of Homoptera: abundance decreased with increasing altitude. Estimate = -0.005, SE = 0.002, t value = -2.079, P = 0.047, df = 27. (b) A significant effect of aspect was detected in the generalised linear model of Heteroptera: abundance was greater on NW than on SE facing slopes. Estimate = -0.600, SE = 0.265, t value = -2.266, *P* = 0.032, df = 27. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 3.2. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 30.

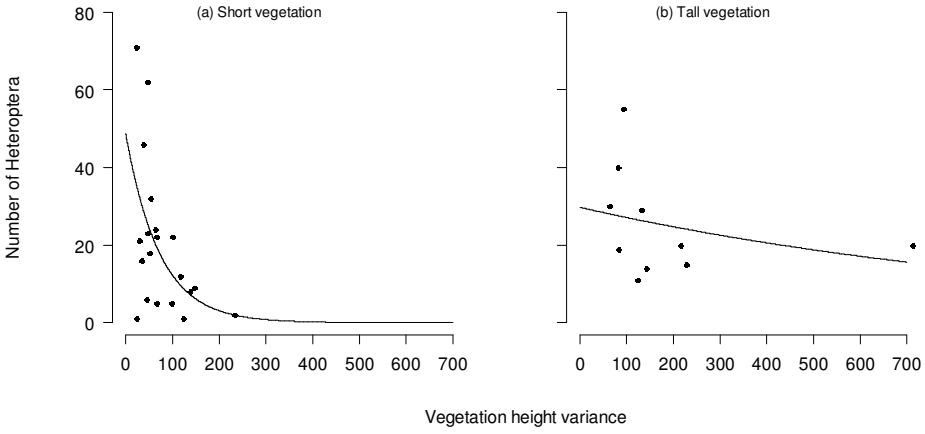


Figure 3. 4 The response of Heteroptera abundance to the interaction between vegetation height variance and vegetation height. Estimate = 0.002, SE = 0.001, t value = 3.738, P = 0.001, df = 27. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 3.2. Short vegetation = ≤ 24 cm, tall vegetation = > 24 cm. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 30.

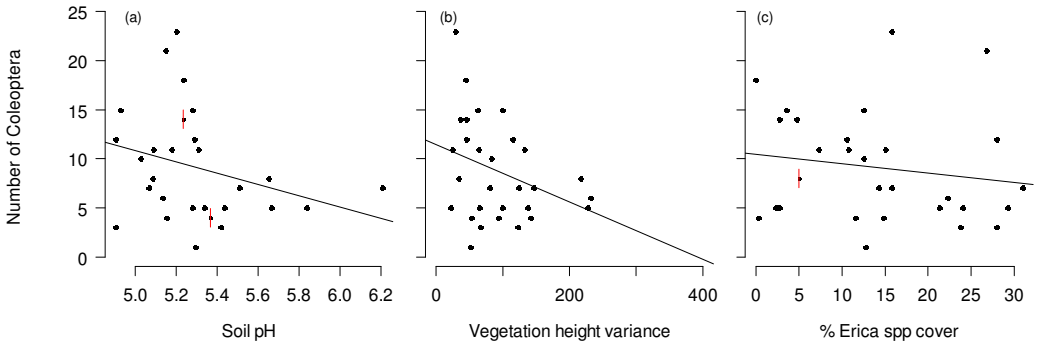


Figure 3. 5 The response of Coleoptera abundance to (a) soil pH, (b) vegetation height variance, and (c) Erica spp. percentage cover. Significant effects of soil pH, vegetation height variance, and % Erica spp cover were detected in the generalised linear model for Coleoptera: abundance declined in response to increases in each variable. Lines drawn are the regression of each relationship. (a) Estimate = 0.891, SE =0.373, t value = -2.391, P = 0.026. (b) Estimate = 0.002, SE = 0.001, t value = 3.423, P value = 0.003. (c) Estimate = -0.035, SE = 0.016, t value = -2.177, P value = 0.041. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 3.2, n = 30.

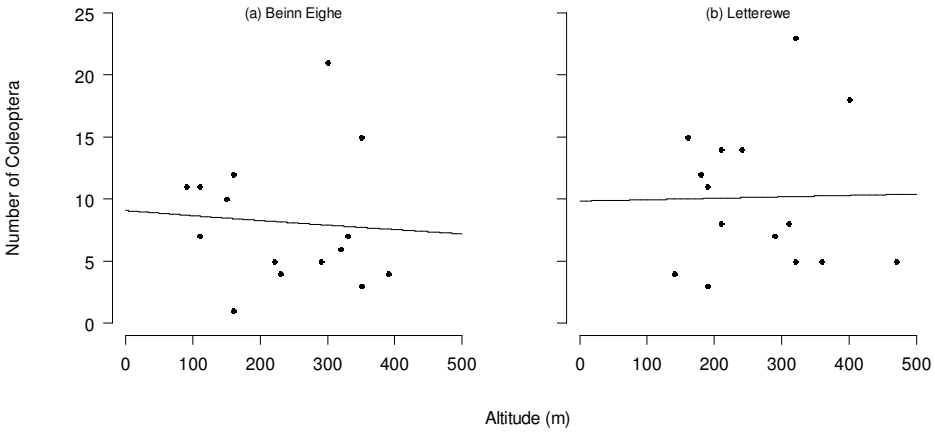


Figure 3. 6 The response of Coleoptera abundance to the interaction between estate and altitude. At Beinn Eighe abundance declined, and at Letterewe increased, with increasing altitude. Estimate = 0.005, SE = 0.002, t value = 2.183, *P* value = 0.041. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 3.2. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002), n = 30.

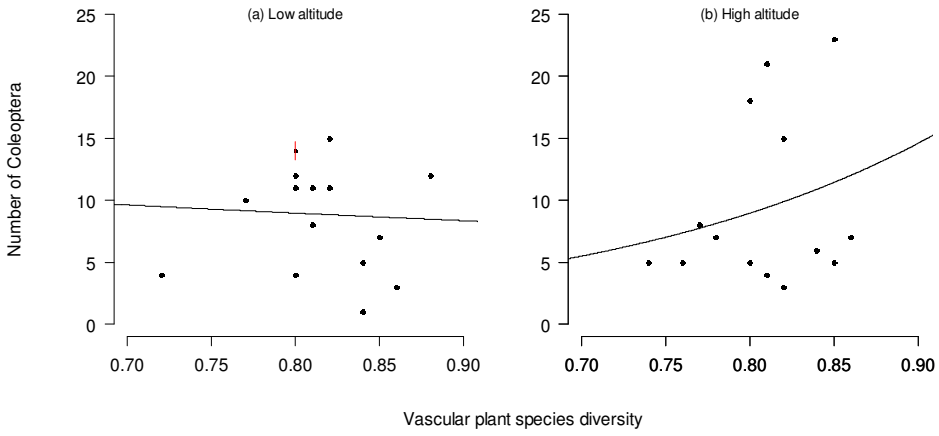


Figure 3. 7 The response of Coleoptera abundance to the interaction between altitude and vascular plant species diversity. At low altitude Coleoptera abundance declined and at high altitude increased in response to increasing vascular plant species diversity (Simpson' D). Estimate = 0.065, SE = 0.029, t value = 2.258, *P* value = 0.035. Low altitude ≤ 280 m, high altitude > 280 m, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that this figure does not take into account all the factors in the full model shown in table 3.2, but is representative of the general underlying relationships. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002), n = 30.

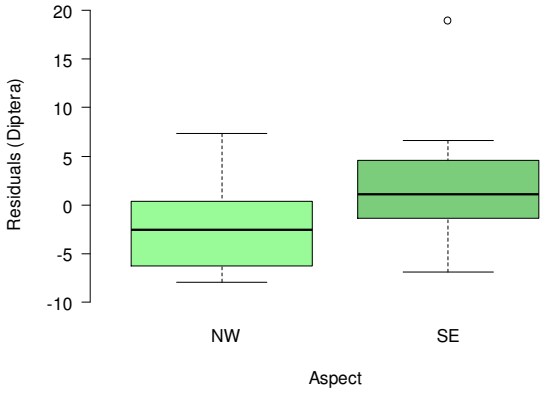


Figure 3. 8 The response of Diptera abundance to aspect. A significant effect of aspect was detected in the generalised linear model: Diptera were more abundant on SE than on NW facing slopes. Estimate = 0.541, SE = 0.212, t value = 2.554, *P* value = 0.017. Note that this figure does not take account of all the factors in the minimal adequate model, but is representative of the general underlying relationships shown in table 3.2. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 30.

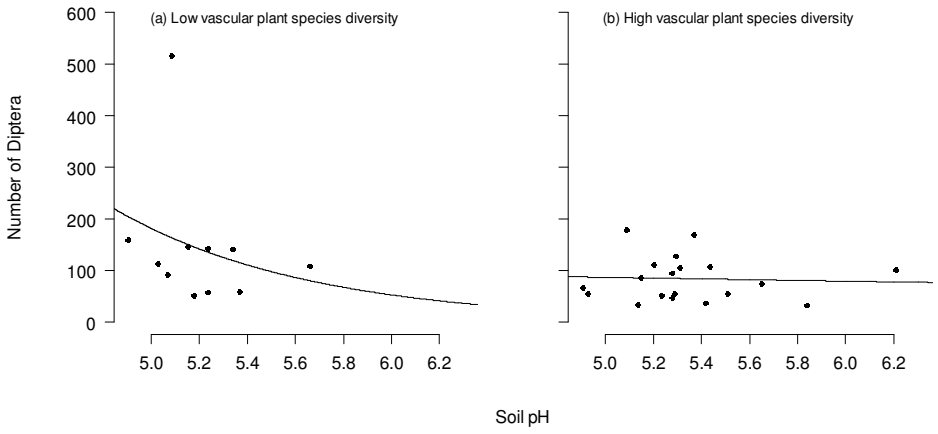


Figure 3. 9 The response of Diptera abundance to the interaction between vascular plant species diversity and soil pH. A significant effect of the interaction between soil pH and vascular plant species richness was detected in the generalised linear model for Diptera. Where vascular plant species diversity (Simpson's D) was low, Diptera abundance declined markedly, and where diversity was high only very slightly, in response to increasing soil pH. Estimate = 35.278, SE = 12.006, t value = 2.938, *P* value = 0.007. Low vascular plant species diversity ≤ 0.8, high > 0.8 , determined using a the CUT function in R. Note that this figure does not take into account all the factors in the full model shown in table 3.2, but is representative of the general underlying relationships. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Note that this figure does not take into account all the factors in the full model shown in table 3.2, but is representative of the general underlying relationships, n = 30.

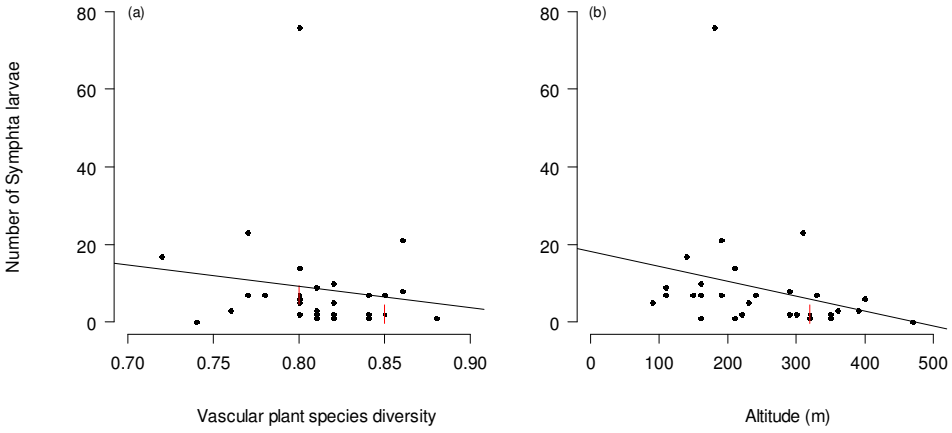


Figure 3. 10 The response of Symphyta larvae abundance to (a) vascular plant species diversity and (b) altitude. Significant effects of vascular plant species diversity (Simpson's D) and altitude were detected in the generalised linear model for Symphyta: abundance declined in response to increases in each variable. Lines drawn are the regression of each relationship. . (a) Estimate = -18.987, SE = 4.581, t value = -4.145, *P* value = 0.001. (b) Estimate = -0.004, SE = 0.002, t value = -2.322, *P* value = 0.029. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 3.2. Lines drawn are regressions of the relationships between the variables, n = 30.

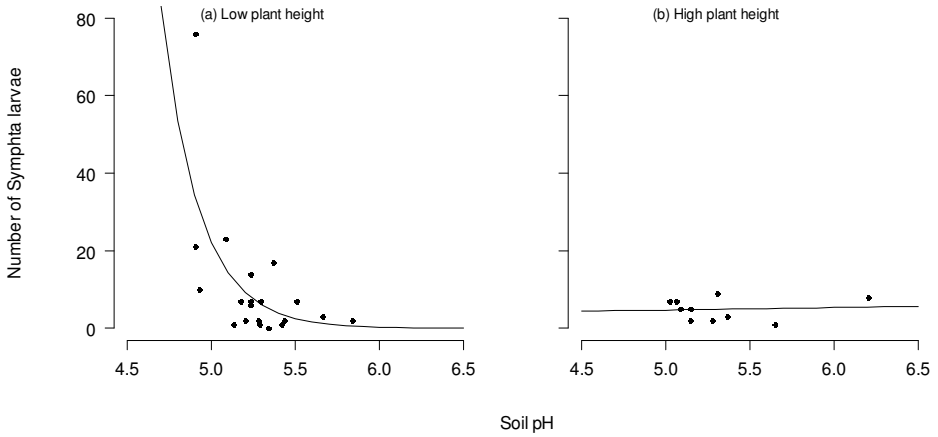


Figure 3. 11 The response of Symphyta larval abundance to the interaction between soil pH and vegetation height. A significant effect of the interaction between soil pH and plant height was detected in the generalised linear model for Symphyta. Where plant height was low (a), Symphyta abundance declined exponentially, and where plant height was high (b) increased very slightly, in response to increasing soil pH. Estimate = 0.563, SE = 0.105, t value = 5.382, *P* value = < 0.001. Low plant height ≤ 24 cm, high > 24 cm , determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that this figure does not take into account all the factors in the full model shown in table 3.2, but is representative of the general underlying relationships. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Note that this figure does not take into account all the factors in the full model shown in table 3.2, but is representative of the general underlying relationships, n = 30.

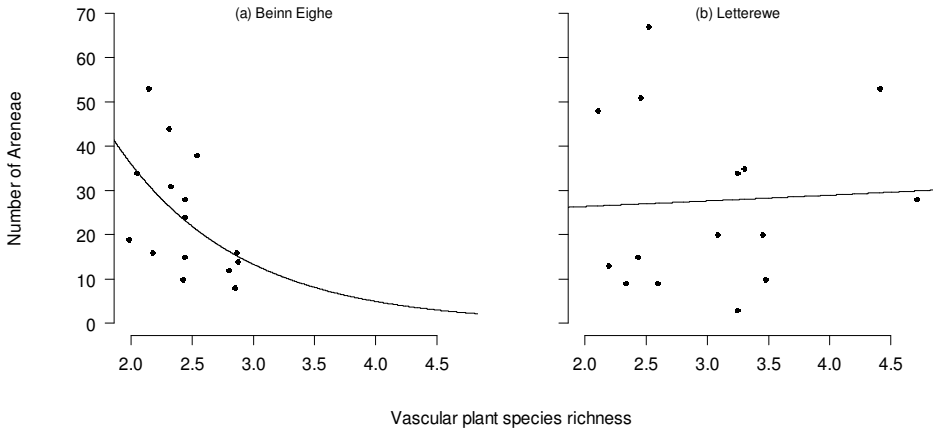


Figure 3. 12 The response of spider abundance to the interaction between estate and vascular plant species richness. The response of Areneae abundance to the interaction between estate and vascular plant species richness (Simpson' D). At Beinn Eighe abundance declined, and at Letterewe increased, with increasing altitude. Estimate = 1.530, SE = 0.561, t value = 2.728, *P* value = 0.004. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 3.2. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002), n = 30.

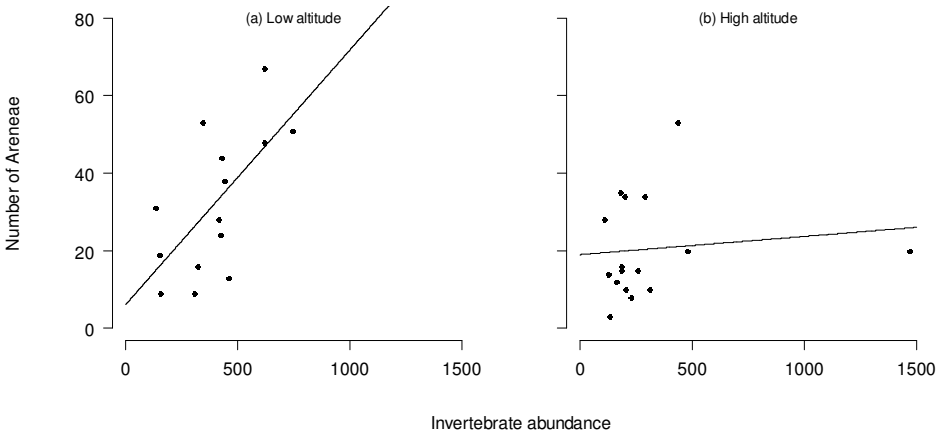


Figure 3. 13 The response of spider abundance to the interaction between invertebrate abundance and altitude. A significant effect of the interaction between invertebrate abundance and altitude was detected in the generalised linear model for Areneae. Estimate = 0.000, SE = 0.000, t value = -3.150, *P* value = 0.004.At low altitude (a) there is a strong positive correlation and high altitudes (b) the correlation is much less pronounced. Low altitude ≤ 280 m, high altitude > 280 m, determined using a linear model to identify the value above and below which splitting the variable was most significant. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 3.2, n = 30.

Table 3. 4 Total counts, means and standard errors (SE) of Lepidoptera larvae species captured, reared and identified from each sampling location at Beinn Eighe and Letterewe, aggregated over four sampling occasions in 2007.

Genus and Species	Common name	Estate					
		Beinn Eighe			Letterewe		
		Total	Mean	SE	Total	Mean	SE
Saturnia pavonia	Emperor Moth	2	0.13 ±	0.09	9	0.60 ±	0.32
Xanthorhoe fluctuata	Garden Carpet	0	0.00 ±	0.00	1	0.07 ±	0.07
Abraxas grossulariata	Magpie	44	2.93 ±	2.31	85	5.67 ±	5.67
Aphelia viburnana	Bilberry tortrix	0	0.00 ±	0.00	3	0.20 ±	0.11
Chloroclysta truncata	Common Marbled Carpet	1	0.07 ±	0.07	0	0.00 ±	0.00
Idaea straminata	Plain Wave	3	0.20 ±	0.14	0	0.00 ±	0.00
Lasiocampa quercus f. callunae	Northern Eggar	0	0.00 ±	0.00	1	0.07 ±	0.07
Macrothylacia rubi	Fox Moth	1	0.07 ±	0.07	1	0.07 ±	0.07
Melanchra pisi	Broom Moth	78	5.20 ±	1.08	96	6.40 ±	3.00
Perizoma didymata	Twin Spot Carpet	0	0.00 ±	0.00	1	0.07 ±	0.07
Perizoma minorata	Heath Rivulet	2	0.13 ±	0.13	0	0.00 ±	0.00
Plusia festucae	Gold Spot	0	0.00 ±	0.00	1	0.07 ±	0.07
Xestia agathina	Heath Rustic	5	0.33 ±	0.13	0	0.00 ±	0.00
Xylena vetusta	Red Sward Grass	0	0.00 ±	0.00	1	0.07 ±	0.07
Morphospecies a	Unidentified	1	0.07 ±	0.07	0	0.00 ±	0.00
Morphospecies b	Unidentified	102	6.80 ±	1.19	267	17.80 ±	5.60

Table 3. 5 Effect sizes and their standard errors of habitat variables on Lepidoptera. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. *t* value: model *t* statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance. Asterisks indicate the level of significance: *P < 0.05 = *, P < 0.01 = **, P < 0.001* = ***.

	Estimate	SE	*t* value	*P*		Res. Dev.	df
Lepidoptera larvae abundance							
Intercept	-1.237	0.431	-2.871	0.008	**	2.794	26
Erica sp. Percentage cover	0.084	0.027	3.118	0.004	**		
Vegetation height	0.083	0.020	4.132	< 0.001	***		
Erica sp. Percentage cover : vegetation height	-0.004	0.001	-2.957	0.007	**		
Lepidoptera larvae species richness							
Estate (Beinn Eighe)	0.850	0.092	9.209	< 0.001	***	3.578	28
Estate (Letterewe)	-0.438	0.131	-3.355	0.002	**		
Lepidoptera larvae species diversity							
Estate (Beinn Eighe)	0.408	0.138	2.956	0.007	**	0.658	24
Estate (Letterewe)	0.652	0.241	2.711	0.012	*		
Molinia caerulea percentage cover	0.006	0.003	1.601	0.122			
Altitude	0.000	0.000	0.536	0.597			
Estate : *Molinia caerulea* percentage cover	-0.022	0.006	-3.584	0.001	**		
Estate : altitude	-0.002	0.001	-3.248	0.003	**		
Broom moth larvae abundance							
Estate (Beinn Eighe)	0.975	1.010	0.965	0.345		31.642	22
Altitude	-0.004	0.002	-2.012	0.057	.		
Vegetation height	0.077	0.029	2.667	0.014	*		
Estate (Letterewe)	5.264	1.057	4.982	< 0.001	***		
Molinia caerulea percentage cover	-0.024	0.012	-2.079	0.049	*		
Aspect (SE)	0.048	0.419	0.115	0.909			
Altitude : estate	-0.022	0.005	-4.071	0.001	***		
Estate : aspect	-2.393	1.063	-2.251	0.035	*		

Notes: Minimal adequate models for (a) Lepidoptera larvae abundance as a function of the interaction between *Erica* spp. % cover and vegetation height. Explanatory variables excluded during model simplification included Soil pH : altitude $P = 0.9$, soil pH : vegetation height variance $P = 0.423$, altitude : vegetation height variance $P = 0.144$, soil pH : estate $P = 0.986$, vegetation height variance : estate $P = 0.466$, altitude : estate $P = 0.170$, soil pH $P = 0.567$, altitude $P = 0.353$, vegetation height variance $P = 0.070$, estate : *Calluna vulgaris* % cover $P = 0.396$, *Erica* spp. % cover : vascular plant species diversity $P = 0.661$, estate : vascular plant species diversity $P : 0.564$, vascular plant species diversity $P = 0.896$, *Erica* spp. % cover : vascular plant species richness $P = 0.432$, estate vascular plant species richness $P = 0.264$, estate : vegetation height $P = 0.306$, estate : *Erica* spp. $P = 0.063$, estate $P = 0.119$, *Erica* spp. % cover : *Molinia caerulea* % cover $P = 0.580$, *Molinia caerulea* $P = 0.882$, vegetation height : aspect $P = 0.852$, aspect $P = 0.782$. Model simplification for all models follows the same protocol as (a). See Chapter Two for a full explanation of each of the explanatory variables. Models of abundance data are Generalized Linear Models's with a quasipoisson error structure, richness and diversity indices are Linear Models with normal errors, n = 30.

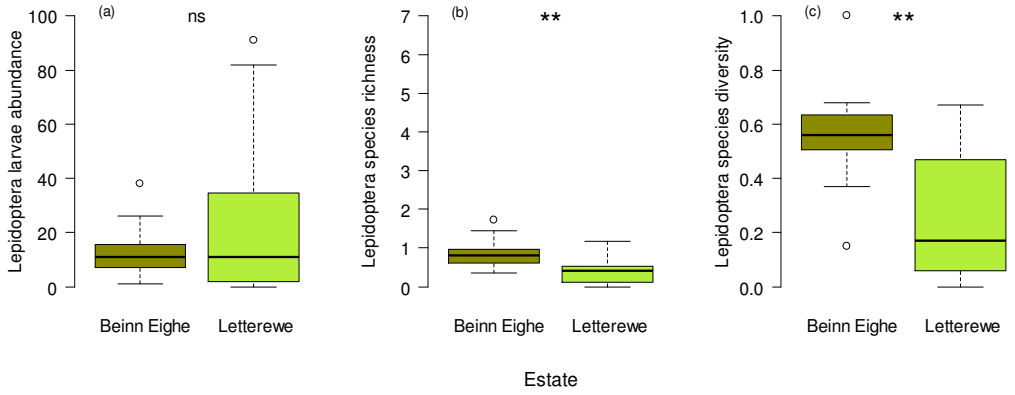


Figure 3. 14 Boxplot illustrating the variation in Lepidoptera larvae (a) abundance, (b) species richness and (d) species diversity collected at sample locations at Beinn Eighe and Letterewe. No significant difference in Lepidoptera larvae abundance, and significant differences in Lepidoptera species richness and diversity were detected in the generalised linear models of Lepidoptera response. Abundance did not differ (a) Estimate = -0.238, SE = 0.147, t value = -1.616, *P* = 0.119, df = 25, richness was lower (b) Estimate = -0.438, SE = 0.131, t value = -3.355, *P* = 0.002, df = 28, and diversity lower (c) Estimate = 0.652, SE = 0.241, t value = 2.711, *P* = 0.012, df = 24, at Letterewe than at Beinn Eighe. Non-significant estimate, SE, *t* and *P* values taken from the relevant model simplification. Boxes show the interquartile range with the median shown as a bold line. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 3.4. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 30.

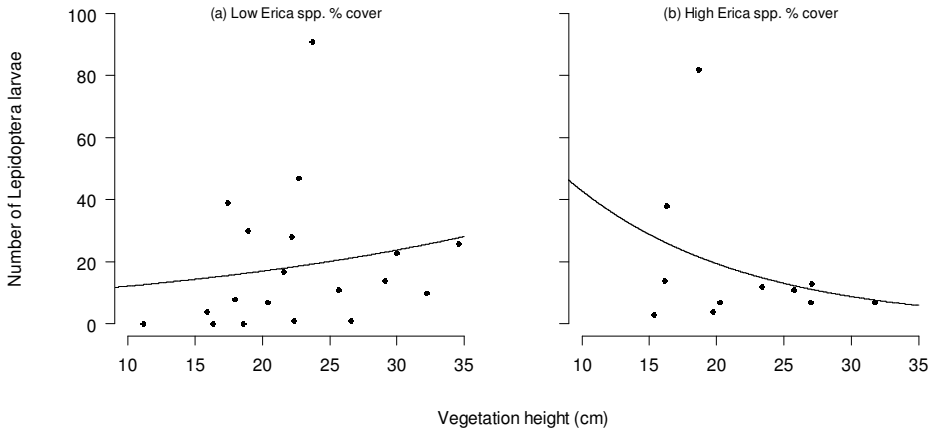


Figure 3. 15 The response of larval Lepidoptera abundance to the interaction between Erica sp. percentage cover and vegetation height. A significant effect of the interaction between vegetation height and Erica spp cover was detected in the generalised linear model for Lepidoptera larvae abundance. Estimate = -0.004, SE = 0.001, t value = -2.957, *P* value = 0.007. At low Erica sp*p* % cover (a) there is an exponential positive correlation and high Erica sp*p* % cover (b) an exponential decline. Low Erica sp*p* cover ≤ 15.5 %, high Erica sp*p* cover > 15.5 %, determined using a linear model to identify the value above and below which splitting the variable was most significant. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 3.2, n = 30.

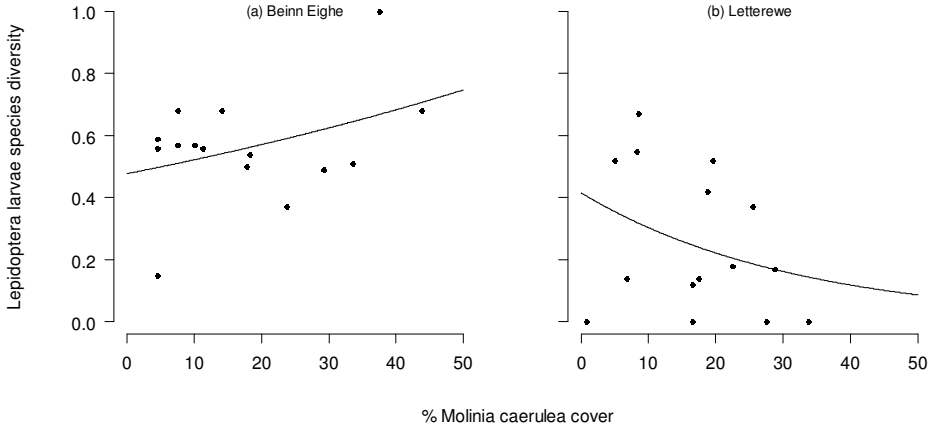


Figure 3. 16 The response of Lepidoptera larvae species diversity to percentage cover of Molinia caerulea at Beinn Eighe and Letterewe. A significant effect of the interaction between estate and Molinia caerulea % cover was detected in the generalised linear model for Lepidoptera larvae species diversity (Simpson's D). Estimate = -0.438, SE = 0.131, t value = -3.355, $P = 0.002$, df = 28. At Beinn Eighe (a) there was a positive correlation and Letterewe (b) a decline. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 3.2, n = 30.

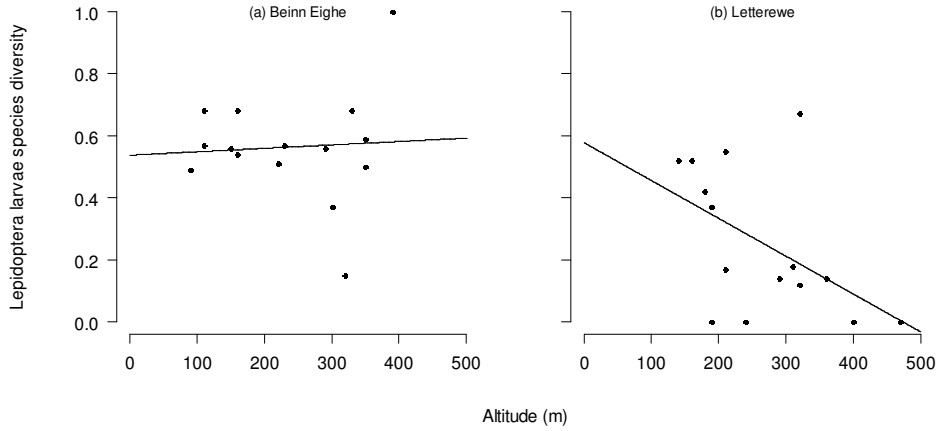


Figure 3. 17 The response of Lepidoptera larval species diversity to altitude at Beinn Eighe and Letterewe. A significant effect of the interaction between estate and altitude was detected in the generalised linear model for Lepidoptera larvae species diversity (Simpson's D): diversity increased very slightly with increasing altitude at Beinn Eighe, and declined dramatically at Letterewe. Estimate = -0.002, SE = 0.001, *t* value = -3.248, $P = 0.003$, df = 24. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 3.4. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002), n = 30.

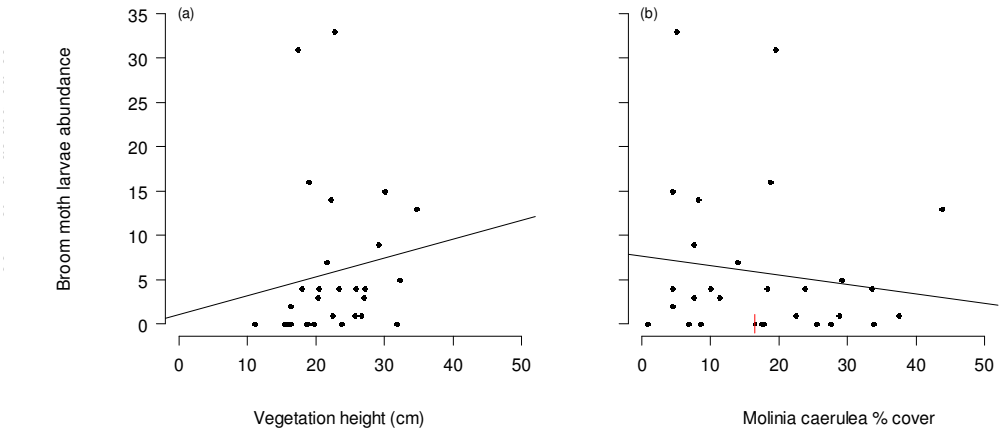


Figure 3. 18 The response of Broom moth larval abundance to (a) vegetation height and (b) *Molinia caerulea* percentage cover. A significant effect of (a) vegetation height and (b) Molinia caerulea % cover was detected in the generalised linear model for Broom moth larvae abundance. Abundance increased in response to vegetation height (a) Estimate = 0.077, SE = 0.029, t value = 2.667, *P* = 0.014, df = 22, and decreased in response to Molinia caerulea % cover (b) Estimate = 0.024, SE = 0.012, t value = -2.079, *P* = 0.049, df = 22. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 3.4. Lines drawn are regressions of the relationships between the variables, n = 30.

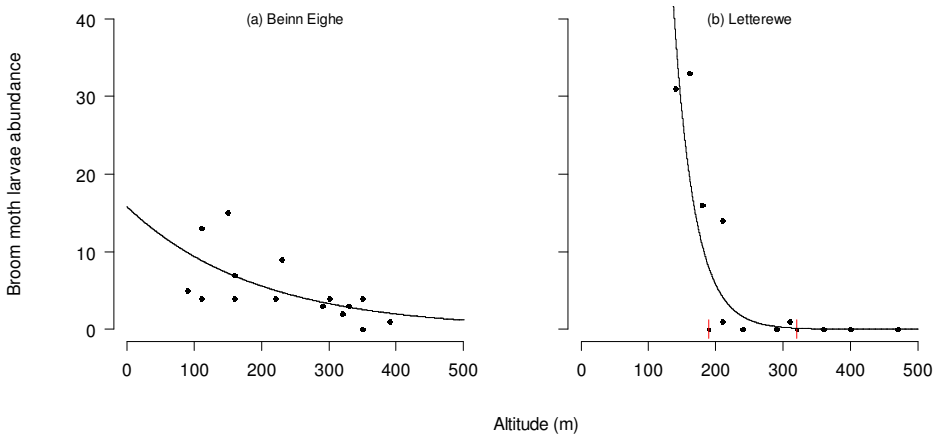


Figure 3. 19 The response of Broom moth larval abundance to the interaction between altitude and estate. A significant effect of the interaction between estate and altitude was detected in the generalised linear model for Broom moth larvae abundance. At Beinn Eighe there was a gradual decline in abundance in response to increasing altitude, and a dramatic exponential decline at Letterewe (a) Estimate = -0.022, SE = 0.005, t value = -4.071, *P* = 0.001, df = 22. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 3.4. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 30.

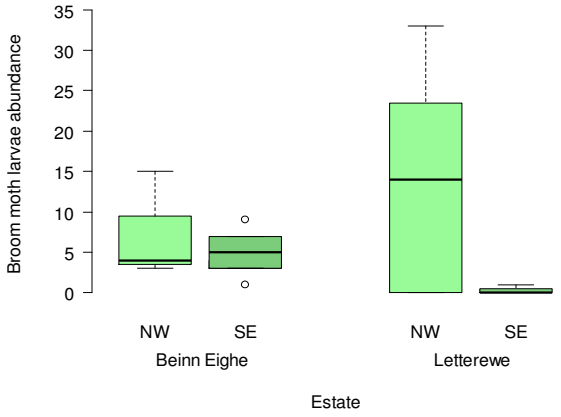


Figure 3. 20 The response of Broom moth larval abundance to the interaction between estate and aspect. A significant effect of the interaction between estate and aspect was detected in the generalised linear model for Broom moth larvae abundance. Estimate = -2.393, SE = 1.063, *t* value = -2.251, *P* = 0.035, df = 22. Note that this figure does not take into account all the factors in the full model shown in table 3.4, but is representative of the general underlying relationships. Note that this figure does not take account of all the factors in the minimal adequate model, but is representative of the general underlying relationships shown in table 3.4, n = 30.

Table 3. 6 Ratios of the variance of the abundance of invertebrate groups captured at each sampling location at Letterewe and Beinn Eighe, aggregated over four sampling occasions in 2007. F value: model F statistic. *P*: model *P* value. df: degrees of freedom. Asterisks indicate the level of significance: *P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***.*

Response	F	df	*P*		Ratio
Homoptera	0.112	14	0.000	*	0.112
Heteroptera	0.412	14	0.108		0.412
Coleoptera	0.818	14	0.712		0.818
Diptera	0.153	14	0.001	*	0.153
Symphyta	0.022	14	0.000	*	0.022
Areneae	0.473	14	0.174		0.473
Lepidoptera larvae	0.104	14	0.000	*	0.104
Lepidoptera species richness	1.184	14	0.756		1.184
Lepidoptera species diversity	0.598	14	0.348		0.598
Broom moth larvae	0.130	14	0.000	*	0.130

At low altitudes (≤ 280 m) Coleoptera abundance showed a slight negative linear response to vascular plant species diversity, while at high altitudes (> 280 m) this relationship was stronger and positive (figure 3.7). The abundance of Diptera was significantly higher on NW than on SE facing sampling locations (figure 3.8), and varied in response to the interaction between soil pH and vascular plant species diversity (figure 3.9). There was an exponential decline in abundance in response to soil pH at low plant diversity values (Simpson's probability ≤ .08) while at higher plant diversity values (Simpson's probability > 0.8) the relationship was more gently negatively liner. The exponential decline at low diversity values is strongly influenced by a single data point, however examination for idiosyncrasy justified its retention in the model. Symphyta larva showed significant negative linear declines in response to both vascular plant species diversity (figure 3.10a) and altitude (3.10b), relationships that were notably uninfluenced by a single outlying data point. An outlying data point is a strong influence on the exponential decline exhibited in response to soil pH at low vegetation height, in contrast to the almost imperceptible positive linear correlation at high vegetation height (figure 3.11). Again examination justified retention of the outlier. The abundance of Areneae was best predicted by two interactions, that between estate and vascular plant species richness (figure 3.12), and invertebrate abundance and altitude (figure 3.13). A steep exponential decline in response to plant species richness at Beinn Eighe contrasts markedly with the gentle positive linear correlation at Letterewe. At low altitudes (≤ 220 m) there is a strong positive linear relationship between spider abundance and invertebrate abundance, uninfluenced by an outlier, but at higher altitudes (> 220 m) this relationship is much less steep.

Lepidoptera larval abundance was predicted by a single significant interaction, between *Erica* spp. percentage cover and vegetation height (figure 3.15). Where *Erica* spp. cover was low, the relationship is gently positively linear, and where cover is high an exponential decline is predicted. The diversity of Lepidoptera larva species was predicted by two significant interactions. At Beinn Eighe the relationship with *Molinia caerulea* percentage cover was positively linear, and at Letterewe negatively liner (figure 3.16). This pattern is mirrored in the response to altitude, but with a far steeper decline at Letterewe (figure 3.17). Broom moth larval abundance showed a positive linear relationship with vegetation height (figure 3.18a) and a negative linear relationship with *Molinia caerulea* percentage cover (figure 3.18b), and was also predicted by two significant interactions. At Beinn Eighe the response to altitude was a gentle negative curve, and at Letterewe a steep exponential decline (figure 3.19). Broom moth larvae were more abundant on NW than SE

facing sampling locations, more so on NW slopes at Letterewe than at Beinn Eighe, while more so on SE facing slopes at Beinn Eighe than at Letterewe (figure 3.20). The ratio of variance of the aggregated abundances of invertebrate groups between the estates was significant for Homoptera, Diptera, Symphyta, Lepidoptera larvae, and Broom moth larvae (table 3.6). For Diptera, Symphyta and Lepidoptera larvae, this was the case even though there was not a significant difference in abundance, and in all cases the variance of each group was greater at Letterewe than at Beinn Eighe.

3.5 Discussion

There was very little variation in the abundance of invertebrates between Letterewe and Beinn Eighe, despite significant differences in grazing pressure from red deer (15 per km^2 and 2.63 per km^2 respectively) and vegetation characteristics. It is most likely that deer have such low impacts on the structure and function of wet heath that even when comparing differences in deer density as pronounced as that between Letterewe and Beinn Eighe, there is no measurable impact on the invertebrate assemblage. Contrary to this argument is the fact that significant impacts of deer management would be expected in comparisons of more productive plant communities such as NVC U4 Greens, that are used by deer disproportionately to their availability, and has been demonstrated for the red deer population on the island of Rum (Virtanen *et al.*, 2002). Typically invertebrate abundance was higher at Letterewe than at Beinn Eighe (Homoptera, Coleoptera, Areneae) or was not significantly different (Heteroptera, Diptera, Symphyta). The only exceptions were a higher abundance of Lepidoptera, and higher species diversity of larval Lepidoptera at Beinn Eighe than at Letterewe. These results represent compelling evidence that, barring these exceptions, the higher population of red deer at Letterewe does not exert a negative impact on invertebrate biodiversity in wet heath, and indeed that for some taxonomic groups it is positively associated with abundance. These findings are consistent with those of other studies that report greater invertebrate abundance, richness and diversity in extensively rather than intensively, and grazed rather than un-grazed habitat (Suominen, 2003, Gonzalez-Megias, 2004, Di Giulio *et al.*, 2001, Altesor *et al.*, 2006). While Letterewe is extensively grazed, deer impacts at Beinn Eighe are considerably lower, with a five-fold difference in density. These results suggest that for many invertebrate groups, Beinn Eighe may be more analogous to un-grazed rather than extensively grazed habitat, due to grazing pressure being insufficient to act as a driver of diversity.

If not deer density, what were the variables associated with differences in invertebrate abundance? The classically demonstrated determinants of invertebrate communities are aspects of three dimensional vegetation structure, botanical composition and plant species richness (Morris and Plant, 1983, Luff and Rushton, 1989, Southwood *et al.*, 1979, Strong *et al.*, 1984). Architectural attributes of plants include height, canopy spacing, leaf, bud and stem shape and size, branching angles, surface pubescences and texture, along with spatio-temporal development and persistence (Lawton, 1983), and it seems likely that invertebrates respond to these attributes. The effect of vegetation structural and species compositional variables was inconsistent between invertebrate groups, and is probably the result of complex interactions with grazing, the contrasting ecologies of the different invertebrate groups examined, and estate specific effects. Invertebrate diversity frequently exhibits a positive relationship with plant biomass, structural complexity (Lawton, 1983, Southwood *et al.*, 1979) and plant species diversity (Siemann et al., 1998) not least because approximately 75% of insect species are phytophagous (Lawton, 1983). Structural variation, particularly *Calluna* height, has been shown to promote invertebrate diversity in moorlands (Gardner *et al.*, 1997). The increase in Broom moth larvae abundance with vegetation height, and of Symphyta and total Lepidoptera larva abundance in the respective interactions support this, and are consistent with the findings of Haysom and Coulson (1998). For many shrubby species such as heathers and bog myrtle that are characteristic of moorlands, there are clear differences in the availability of resources offered by plants along an age gradient. *Calluna*, for example has a thick layer of litter used by overwintering Lepidoptera pupae, which is not available under younger pioneer plants (Haysom and Coulson, 1998).

Lepidoptera species diversity and adult abundance were exceptions to the general trend, being higher at Beinn Eighe than at Letterewe. Vegetation was taller and structurally more variable at Beinn Eighe, and this pattern fits the large body of empirical evidence (Haysom and Coulson, 1998, Strong *et al.*, 1984, Lawton, 1983). The majority of the Lepidoptera species sampled (65%) are herbivores of *Calluna* and/or *Erica. Calluna* cover did not differ significantly between estates, however *Erica* cover was significantly higher at Beinn Eighe. Larval preference for *Erica* over *Calluna* may be responsible for this observation. Altitude often determines Lepidoptera assemblages (Haysom and Coulson, 1998), however the mean height above sea level of sampling locations was not significantly different between estates.

The most likely explanation for the difference observed in the variance of the abundances of invertebrate groups between the estates is probably due to the effects of grazing at Letterewe. The variation in vegetation structure and composition this causes is reflected in invertebrate abundances, even for groups where overall numbers do not differ between the estates. Where grazing pressure is higher, impacts on vegetation were greater; vegetation was significantly taller at Beinn Eighe, and significantly more species rich at Letterewe. Invertebrates were either unaffected or benefit from the resulting increase in habitat heterogeneity. Optimal foraging theory provides a candidate model with which to explain the absence of a detrimental effect of higher rather than lower grazing pressure at Letterewe. In order to maximise their nutritional intake, red deer preferentially select certain habitat types over others. At Letterewe, Greens (U4), Dry Heath (H10), and Course Grassland (U5) are used most heavily, and Wet Heath (M15) only lightly (Milner *et al.*, 2002), although Wet Heath is the dominant plant community at both Letterewe and Beinn Eighe (> 50 % cover). This observed patterned fits well the predictions of the Ideal Free Distribution (IFD) model in which organisms are predicted to distribute themselves such that resource use matches availability (Kennedy and Gray, 1993). The under-represented yet preferred habitat types probably act as a buffer to grazing pressure, allowing the maintenance of the overall condition of the habitat, and the higher grazing pressure as a driver of plant and invertebrate biodiversity throughout areas where less profitable patches are utilised.

3.5.1 Synthesis and applications

Concern over increasing deer numbers (Clutton-Brock *et al.*, 2004b, Bardgett *et al.*, 1995) with the implication of increasingly severe detrimental effects, has lead to conflicting objectives between conservation and deer managers, the former often seeking to reduce deer numbers and the later to maintain or increase them. This study provides little evidence of negative impacts on the more heavily grazed Letterewe estate, suggesting that at the current density, the deer population is not a cause for concern with respect to invertebrate biodiversity. The deer population is food limited and regulated by winter mortality, and stalking acts as a surrogate for natural regulation by top predators (Milner *et al.*, 2002). Several invertebrate groups responded positively to plant structural and diversity characteristics. Increasing habitat heterogeneity at small spatial scales within estates is often a good way of benefiting arthropod diversity and abundance, as demonstrated for the number and abundance of arthropod species in grazed grasslands (Dennis *et al.*, 1998).

Traditional methods of moorland management such as muirburn that favour grouse, produce mosaics of habitat patches, particularly stands of *Calluna* of varied age class and structural heterogeneity, that also benefit the distinct carabid assemblages associated with each (Gardner *et al.*, 1997). Benefits to other taxa are likely as well, however muirburn is not practical on a large scale at Letterewe. Grazing has a similar effect through its action of reducing vegetation height, as shown in this study, creating a more open canopy. The amount of grazing pressure is crucial, since too high a level can reduce the occurrence of mature heather stands and leave areas vulnerable to invasion by bracken and mat-grass (Thompson et al., 1995) reducing the availability of characteristic moorland habitat types. Increased uniformity of *Calluna* stands and area of standing crop in building and mature phase can reduce the abundance and diversity of carabid and other invertebrate assemblages (Gimingham, 1985a) and the presence of *Calluna* in all phases of development, potentially driven by grazing, would increase invertebrate diversity. Moorland bird species depend predominantly on an invertebrate diet, consisting of very few taxa, including Arachnida, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Oligochaeta, of which the beetles and flies are most important (Buchanan et al., 2006). Sheep grazing is thought to impact moorland birds though reduction of preferred vegetation types, changes to food supplies and alteration of predation pressure (Fuller and Gough, 1999). Birds are unlikely to be negatively impacted by deer grazing, which is very different to that of sheep, at the deer population densities observed in this study. In fact they may be benefited at Letterewe were invertebrate abundance was higher in some cases, although this is cautious speculation as many moorland birds feed on subterranean invertebrates not considered here. *Molinia* cover did not vary significantly between estates, providing no evidence of its replacement of more palatable plant species as can happen under heavy grazing pressure, and considered undesirable in moorland management as it prevents development of dwarf shrub communities (Marrs *et al.*, 2004).

3.5.2 Limitations

While sweep sampling is an effective method of sampling for many invertebrate species, particularly those associated with above ground vegetation, these are a small fraction of total invertebrate species and the conclusions on the impact of grazing on diversity made here are cautious. Many similar studies favour the use of motorised suction samplers, however the logistical constraints of working in the study area rendered this method impractical, and sweep netting is considered an effective alternative (Janzen, 1973,

Southwood and Henderson, 2000). Lepidoptera diversity was significantly different between the estates, and other species level differences may be observed if identification was carried out for other invertebrate groups i.e. Hemiptera (Hartley, 2003). The limitation of not identifying all species are such that conclusions on the specific ecologies of host plant – invertebrate interactions are not possible, however under the practical constraints of this study examination of higher taxonomic groupings produces meaningful results. This study only looked at variation in invertebrate response during a short period of study, and it is possible that the effects of the various explanatory factors would become clearer over a greater temporal scale. Temporal trends however are not apparent over the length of short studies such as this, and are therefore not considered. The practical limitations of this study were such that only two moorland estates could be compared, with obvious implications for sample size, however such comparisons have yielded useful results in other studies (Hartley, 2003).

3.6 Conclusions

Despite significant variation in deer numbers and vegetation, the abundance of moorland invertebrates between Letterewe and Beinn Eighe was predicted variously by a range of habitat variables, but the anticipated effect red deer grazing pressure was only important in determining two aspects of the Lepidoptera assemblage. Habitat heterogeneity was the most important predictor of invertebrate response. This study contributes to the increased understanding of grazing influences on moorland habitats, in the underrepresented area of wild ungulate impacts on invertebrates. Invertebrates are an essential component of conservation priority of moorlands, and this work highlights the need for science to inform land management policy that must often seek to balance conservation objectives with economic interests. A one size fits all policy may not be appropriate in all applications, and site specific or more informed customised approaches to land management may produce more effective and favourable benefits both to the conservation of biodiversity and economic land use objectives. This study supports the notion that a red deer herd of a size consistent with viable stalking interests can be integral to the maintenance of heather moorland biodiversity.

Chapter 4

Invertebrate diversity, richness and abundance in the Letterewe oak woodland: responses to grazing management

Abstract

Chapter Four details the results of an experimental investigation into red deer grazing impacts on the invertebrate assemblage in the Letterewe oak woodland. Grazing can have either positive or negative impacts on ecosystems, and it is important to have specific knowledge of such effects in order to inform habitat management policy. Invertebrates were either positively affected or unaffected by grazing, despite significant effects on the vegetation. There were no instances of negative grazing impacts on any of the studied invertebrate responses. The continued use of short-term rotational grazing exclosures is recommended to facilitate the duel aims of maintaining biodiversity and allowing natural tree regeneration in the Letterewe oak woodland.

4.1 Introduction

The selective action of grazing and browsing by large herbivores can have a profound impact on vegetation communities, with knock on effects for co-dependent elements in an ecosystem (Stewart, 2001; Suominen, 2003). As terrestrial invertebrates respond to habitat modification, they are hypothesised to be sensitive to grazing and browsing. Increased habitat modification through management, disturbance or modification can lead to declines in species richness (Lawton, 1998) as these impacts may alter plant species composition, structural complexity, microhabitat, decomposition and litter accumulation, all of which may impact invertebrates (Suominen, 1999). Woodlands are one of the richest habitats for

invertebrate species in the UK due to the structural and species diversity of the vegetation, which creates a large number and variety of niches (Stewart, 2001, Petit and Usher, 1998). Woodlands also provide important shelter for livestock and wild deer, particularly during the harsh winter months (Baines *et al.*, 1994, Milner *et al.*, 2002).

4.1.1 The role of herbivory in woodlands

Modern woodlands are incomplete ecosystems in that they now lack top carnivore species, and historically herbivores have been integral and beneficial to woodland ecology (McEvoy *et al.*, 2006, Suominen, 1999, Stewart, 2001, Vera, 2000). Large herbivores have exerted selection pressure on the growth, life history, and physiological characteristics of plants, which have co-evolved with the influence of grazing and browsing over thousands of years (McEvoy *et al.*, 2006, Putman, 1996). Although they are the primary large wild herbivore in UK woodlands, deer actually remove a much smaller percentage of annual primary productivity in woodlands than do invertebrate herbivores (Stewart, 2001). Exclusion of large herbivores can lead to significant reductions in the abundance and diversity of plant and animal communities in woodlands (McEvoy et al., 2006). Whether wild or domestic, grazing mammalian herbivores are often seen as useful elements in woodland conservation management prescriptions (Pollock et al., 2005) and can facilitate the maintenance and enhancement of woodland floral and faunal diversity (McEvoy et al., 2006). They can play a fundamental role in determining the architectural structure and species composition of vegetation, which provides habitat and food resources for a substantial range of invertebrates, and where deer alter the species or structural composition there are likely to be considerable consequences for invertebrates (Stewart, 2001). Large herbivores create and maintain open areas and clearings, and reduce shade, allowing shade intolerant species to persist (Stewart, 2001, Vera, 2000). Browsing reduces stem density and limits height growth and foliage density, leading to a more open understory with greater light penetration, allowing more growth at ground level, and benefiting thermophilous invertebrate species that require flowers and/or pollen (Stewart, 2001). The maintenance of ancient parkland and wood-pasture which supports a diverse fauna and flora is achieved though prevention of successional vegetation development by grazing (Stewart, 2001, Putman, 1996, Vera, 2000), and large herbivores such as deer have a direct effect on dung feeding species of invertebrates through faecal inputs, which in turn helps to maintain birds, bats (Stewart, 2001) and other mammals such as badgers, foxes and small mammals.

4.1.2 Mechanisms of impact and the response of invertebrates

The effects of habitat modification by grazing will depend on the species and density of deer (Stewart, 2001, Putman, 1996). The high species richness of woodland invertebrate fauna results in part from the structural diversity of the habitat (Southwood et al., 1979), and indeed many studies report increased biodiversity with increasing structural complexity of the habitat (Haenke *et al.*, 2009, Lawton, 1983). As such, any simplification of this structure due to grazing is likely to lead to reductions (Stewart, 2001, Milner *et al.*, 2002). The modification of sward height and grazing regime (Dennis *et al.*, 1997), *Calluna* height and development phase (Gardner *et al.*, 1997), and vertical stand structure (Humphrey *et al*., 1999) have all been shown to affect epigeal invertebrate assemblages. Reindeer grazing alters vegetation structure (Suominen, 2003), and in the understory, bramble *Rubus fructicosus* is preferentially browsed by deer, the dead and broken ends of stems providing nest sites for rare solitary bee species (Putman, 1986). Grazing can also result in altered palatability of vegetation to invertebrates due to plant chemical processes (Gonzalez-Megias, 2004).

Increased botanical diversity may result from a disturbance such as grazing that reduces the competitive ability of dominant species or by creating habitat patches at varied successional stages (Rambo and Faeth, 1999, Milner *et al.*, 2002). Increased plant diversity was observed following the decreased dominance of lichen grazed by reindeer (Suominen, 2003). Removal of the understory vegetation by grazing drastically alters microclimatic conditions, especially in the epigeal layer, by increasing the penetration of solar radiation which alters light and temperature conditions, increases wind speed, and reduces humidity (Stewart, 2001). Grazed woodland may be warmer and drier in summer than it otherwise might be, due to the increased penetration of solar radiation and wind velocity, and decreased tree density results in reduced litter accumulation, lowering moisture at ground level. Beetles, in particular epigeal species, respond to alterations in microclimate due to habitat modification (Grimbacher *et al.*, 2006, Suominen *et al.*, 2003), and saproxylic species that require dead wood in partial shade, may be affected where these conditions become scarcer when the sheltering effect of herb layer vegetation is removed by browsing (Stewart, 2001). Deer may compete directly or indirectly with invertebrates, directly by competing with phytophagous invertebrates for food resources, indirectly by influencing the abundance of their predators, or may inadvertently prey on the eggs or larvae of invertebrates present on forage vegetation (Baines *et al.*, 1994, Stewart, 2001, Gonzalez-

Megias, 2004). White Admiral butterflies oviposit on honeysuckle within a specific height range in the herb layer that is lost due to browsing by muntjac deer, resulting in both competition for a structural resource, and accidental predation (Stewart, 2001). Soil organic content and wetness are important determinants of carabid communities (Gardner *et al.*, 1997), both of which may be altered by habitat modification through grazing, and reindeer grazing has been shown to alter fine root structure and biomass (Suominen, 2003). Removal of nutrients through feeding, and their deposition through urine, dung, and carcasses may create small localised areas of enrichment, and while not as concentrated as the effect of herbivores that habitually use latrines such as rabbits, may still be important in structuring plant and animal diversity (Stewart, 2001, Milner *et al.*, 2002). The damp patches of mud around small temporary water bodies caused by trampling provide microhabitats for many dipterous species, including hoverflies (Stewart, 2001). The production of large quantities of dung by deer provides resources for a diverse coprophagous fauna, considered in greater detail in Chapter Five, and there are direct effects of deer on their commensals and parasites (Stewart, 2001).

4.1.3 Detrimental effects of grazing

Large herbivores in woodlands can have detrimental effects such as overgrazing and prevention of natural tree regeneration, the properties of which are determined by the intensity of grazing (Pollock *et al.*, 2005, Milner *et al.*, 2002, McEvoy *et al.*, 2006). The reduction or elimination of palatable or grazing intolerant species may reduce botanical diversity, and lead to expansion of grazing tolerant species, rank grasses and bracken (McEvoy et al., 2006). It is interesting to note that of a number of species identified as characteristic of either grazed or un-grazed woodland by McEvoy *et al.,* (2006), most of those that occur at Letterewe are present both in grazed and un-grazed plots (see table 4.1). The abundance and species richness of terrestrial gastropods in boreal forests was reduced in response to grazing, an effect attributed to microclimatic alteration (Suominen, 1999). The rate of litter decomposition and nutrient cycling may be reduced, influencing the availability of nutrients on the soil surface (Stewart, 2001; Tadey and Farji-Brener, 2007). Livestock grazing has been shown to alter nutrient availability on the soil surface indirectly, through effects on the quality of leaf-cutter ant refuse dumps, mediated through the alteration of vegetation community dynamics (Tadey and Farji-Brener, 2007). Removal of low hanging branches by deer is noted as a cause for concern that resulting microclimatic alteration may have detrimental impacts on populations of a rare whorl snail

(Stewart, 2001). To my knowledge, one of only two studies to date to specifically consider the impact of red deer grazing in woodland in the UK or elsewhere examines vegetation and invertebrate communities in native Scottish pine woodland (Baines *et al.*, 1994). Lepidoptera, Hymenoptera, Coleoptera, Areneae, Diptera and Plecoptera were all more abundant in grazing exclosures than grazed woodland, and grazed plots had lower heather and higher grass cover than exclosed or less heavily grazed plots. Bilberry cover was not affected, however selective feeding by deer lead to a reduction in biomass in grazed plots, which may explain the difference in Lepidoptera numbers. Winter grazing of bilberry by red deer was found to affect carabid beetle species assemblages across a gradient of grazing pressure, the effect of which was to alter the microclimatic conditions in the ground and herb layer, resulting in distinct carabid assemblages along the gradient of grazing (Melis *et al.*, 2006). Many rare woodland Diptera suffer under conditions of increased solar penetration, as they require moist humid conditions for larval development, provided by a dense canopy, bushy shrub layer, and lush herb layer, that are lost above a critical grazing threshold (Stewart, 2001).

4.1.4 Beneficial effects of grazing

Many studies of grazing on plant communities indicate that grazers tend to increase plant diversity in accordance with the intermediate disturbance hypothesis (Grime, 1979), although this effect is confounded with the availability of nutrients in ecosystems (Suominen, 2003). Grazing can increase botanical diversity, reduce cover of competitive dominants such as bramble, bracken and rank grasses, and increase ruderal species cover (McEvoy et al., 2006). Conversely, exclusion of large herbivores can lead to significant reductions in the abundance and diversity of plant and animal communities in woodlands, and facilitate coexistence of potential competitors (McEvoy et al., 2006). Grazing and trampling facilitate energy flow, leading to low levels of litter accumulation and rapid decomposition rates, and large mammalian herbivores may introduce immigrant species through seed dispersal on bodies, hair, between hooves, or dunging (McEvoy et al., 2006). Grazing can promote the establishment of Atlantic bryophytes, which are common in the Letterewe oak woodland, and thrive in the absence of competition from field layer species, however tussocks and cushions may be damaged or dislodged under heavy grazing (McEvoy et al., 2006). Epigeal Carabidae and Curculionidae are more species rich and diverse in reindeer grazed forest plots than un-grazed plots, and some species are found only in grazed plots (Suominen, 2003). Diversity was maximised at intermediate grazing

intensity, and mediated by the effects of grazing on lichen cover. Interpreting these results, the author suggests that greater carabid abundance in grazed plots is a reflection of their requirement of more open habitat for hunting, while reduced abundance of Curculionidae is caused by reduced availability of deciduous vegetation as a result of grazing. Increased solar radiation as a result of grazing effects has beneficial impacts for many woodland butterfly species, assuming host and food plants are not adversely affected (Stewart, 2001). While heavy grazing pressure can have drastic detrimental effects for organisms occupying a wide variety of niches, some species have the potential to respond positively to these effects. Where bare ground patches are juxtaposed with sunny clearings, suitable nest site conditions may be provided for solitary bees and wasps (Stewart, 2001). An exclusion experiment in the Sierra Nevada National Park in Spain exhibited greater abundance, biomass, diversity, and composition of epigeal arthropods in ungulate grazed than un-grazed plots (Gonzalez-Megias, 2004). An indirect effect of browsing by Beavers was observed by Martinsen *et al.,* (1998) who noted that Cottonwood re-growth following browsing contained higher concentrations of phenolic glycosides used by chrysomelid leaf beetles as defensive compounds. Beetles fed on re-growth were better defended, and also grew faster and larger due to increased nitrogen content. Studies on the carabid beetle assemblages of plantation forests found higher species richness in open spaces compared to closed canopy patches (Butterfield et al., 1995).

An extreme example of the effect of exclusion is illustrated by a study in the New Forest, Hampshire (Putman et al., 1989). Outside of exclosure plots deer densities were ~100 deer km^{-2} and impacts on regeneration and the understory dramatic. Over a 22 year period the ground beetle assemblage was distinctly altered, with *Pterostichus madidus* more abundant in grazed plots, *Nebria brevicollis* restricted to grazed plots, and *Abax parallelopipedus* and *Carabus violaceous* more abundant in un-grazed plots. This is reflective of the fundamental ecology of these species, all of which are habitat generalists, but the latter two are more associated with a dense herb layer and closed canopy. Leaf litter invertebrates were unaffected by deer browsing, and the extent of the litter unchanged in a large scale natural experiment of overabundant deer in British Columbia, Canada, however litter quality was altered (Allombert *et al.*, 2005b). In a study of *Calluna* heathland in the North York Moors National Park, UK, carabid species associated with shady damp conditions had reduced abundance in heavily grazed heather moorland, where grazing reduced the shading and moisture retention properties of the heather canopy (Gardner *et al.*, 1997). Species richness was also similarly affected. Grazing is hypothesised disrupt

plant-insect interactions through a 'trophic level' hypothesis (Price et al., 1980), and habitat management such as grazing manipulation may alter insect communities through a range mechanisms such as vegetation growth, architecture and diversity (Kruess, 2002, Strong *et al.*, 1984). Short term impacts are linked to reduction of architectural complexity and the associated loss of feeding niches, while longer term impacts arise due to alteration of vegetation community composition and structure (Kruess, 2002).

4.1.5 Grazing, invertebrates and the herb layer

Plant species richness has been shown to affect pollinator richness and the frequency of pollinator visits, including hoverflies, as a result of enhanced spatial and temporal availability of pollen and nectar resources (Ebeling et al., 2008), and flower density to affect hoverfly density and diversity (Haenke et al., 2009). Where grazing impacts influence plant communities this may be expected to also have implications for the associated hoverfly assemblage. Extensively rather than intensively grazed grassland had higher species richness of four insect taxa including parasitoids, the best predictor of which was vegetation height (Kruess, 2002). A study of Irish plantation forests found almost 80 % of the hoverfly species to be associated with open space rather than closed canopy forest (Gittings et al., 2006). Flying Diptera are affected by microclimatic conditions such as wind speed and solar radiation (Peng et al., 1992) and where there is structural variation in vegetation characteristics microclimatic conditions may be altered and cause habitat preferences to be observed in Diptera and other flying insects.

Alteration of plant species composition in the herb layer is driven by selective grazing on palatable species, avoidance of unpalatable species, and stimulation of shade intolerant species through the opening or removal of higher layers (Stewart, 2001). Many host specific insect herbivores are obligatley dependent on common herb layer plants such as violets *Viola* spp*,* enchanters nightshade *Circaea lutetiana,* and dogs mercury *Murcurialis perennis,* while others, including hoverflies and other pollinator species rely on various physiological conditions of herb layer plants such as flowering status, stature and microclimate (Stewart, 2001).

Plant architectural diversity is predicted to increase species richness of herbivorous invertebrate hosts of parasitoids (Fraser *et al.*, 2007, Strong *et al.*, 1984), leading these authors to hypothesise that habitats with greater plant species richness and vegetation architecture will support a richer parasitoid fauna, with some empirical evidence provided

by Fraser *et al.,* (2008b). Increased hoverfly diversity with increased structural complexity was reported by Haenke *et al.* (2009).

Bramble, *Rubus fructicosus,* is an important element of the herb layer that is preferentially browsed by deer early in the growing season. Its flowers provide important pollen and nectar resources for a wide range of insects such as hoverflies, including *Criorhina* spp., whose larvae are saproxylic. The limited dispersal capabilities of these species render them dependent on dead wood sources and open flower rich rides or clearings, of the type maintained by grazing (Stewart, 2001). Other important floral resources eaten by deer include hawthorn *Crataegus monogyna,* blackthorn *Prunus spinosa,* elder *Sambucus nigra,* and species of the Umbelliferae and Compositae (Stewart, 2001). Heavy deer grazing pressure in the herb layer is likely to result in the removal of important host plant species, their replacement with unpalatable gramminoids and bracken, leading to overall reductions in invertebrate richness (Stewart, 2001).

The basic habitat needs of parasitoids include a host population, host food plants, adult food sources, and diapause, roosting, shelter and mating sites (Shaw, 2006), all of which may feasibly be altered by the action or absence of grazing on the vegetative habitat. Species richness and architecture of vegetation were predicted to increase niche availability for herbivores and their parasitoids (Hawkins, 1988) potentially as a result of alteration of the cues that parasitoids use for host location (Saaksjarvi et al., 2006), while there is empirical evidence that herbivore mediated production of plant volatiles may play a role in attracting different parasitoid species (Godfray, 1994). The increasingly complex architecture of herbivore host plants along the gradient of grasses, herbs, shrubs and trees, significantly affected insect (Lawton and Schroder, 1977) and parasitoid species richness (Hawkins and Lawton, 1987; Hawkins, 1988) on host plants, and tree species richness and density was correlated with parasitoid diversity (Sperber et al., 2004). Evidence of a correlation between plant species richness and parasitoid species richness was observed by (Saaksjarvi *et al.,* 2006) although the weak nature of the relationship led the authors to speculate that the observed pattern may be more likely a result of increased plant functional group richness and architectural complexity. Searching behaviour of parasitoids is affected by the architecture of prey host plants; plant size, height, leaf number, leaf surface area, and branch number were negatively correlated with the attack rate of a parasitoid of the citrus mealybug (Cloyd and Sadof, 2000). In a rare example of an anthropogenic disturbance affecting a tertiary trophic level, indirect and direct effects on host-parasitoid interactions in cattle grazed verses cattle un-grazed woodland were

observed in a study by Vanbergen *et al.,* (2006). Grazing dependent habitat variation resulting in increased species richness and cover in the herb layer vegetation, led to a doubling of the parasitism rate in the grazed habitat for a herbivore-parasitoid interaction. Humphrey *et al.,* (1999) found vertical stand structure was correlated with higher field layer cover, which supported greater syrphid diversity, but lower carabid diversity.

4.2 Rationale for this study

There are relatively few studies on the impact of wild ungulate grazing on invertebrates in the epigeal and herb layers of the UK's native woodlands (Baines *et al.*, 1994, Rambo and Faeth, 1999, Putman *et al.*, 1989, Suominen, 2003, Melis *et al.*, 2006), but grazing is known to alter the abundance, richness and distribution of invertebrates in the epigeal layer (Dennis, 2002; Suominen, 2003). Use of one group of invertebrates as an indicator of general trends across invertebrate groups is desirable but not consistent, as a measure of the impacts of habitat modification (Lawton, 1998). Carabidae and Staphylinidae have been effectively used to quantify the impacts of grazing regimes in *Nardus stricta* grasslands (Dennis *et al.*, 1997) and heather moorland (Gardner *et al.*, 1997), and woodlands are important habitat for many relict epigeal invertebrate species (Sroka and Finch, 2006). Managers of woodland grazed by wild herbivores must seek to implement effective policies for the maintenance of habitats in favourable condition. This study is intended to investigate the impacts of red deer grazing management in Atlantic oak woodland, for which there is a particular paucity of empirical research, in order to help create an evidence base on which managers can found sound policy decisions.

Table 4. 1 Average percentage ground cover including flora in grazed and un-grazed treatment plots in the Letterewe oak woodland.

Ground cover	Grazed	Un-grazed
Acer pseudoplatanus	0.07	0.07
Agrostis capillaris	0	0
Alnus glutinosa	0.05	0
Anemomone nemorosa	0	0
Betula pendula (Betula sp.)	1.52	1.98
Blechnum spicant	7.90	9.45
Brachypodium sylvaticum	0	0
Calluna vulgaris	11.76	11.76
Comopodium majus	3.10	3.07
Corydalis claviculata	0.00	0.00
Crataegus monogyna	0.38	0
Deschampsia cespitosa	0	0
Deschampsia flexuosa	5.21	5.21
Digitalis purpurea	0	0
Erica cinerea	0.81	1.32
Erica tetralix	0.41	0.41
Fragaria vesca	0.75	0.52
Fraxinus excelsior	4.27	1.38
Galium saxatile	2.19	2.47
Hedera helix	0	0
Hyacinthoides non-scripta	4.07	4.22
Hypericum pulchrum	2.16	2.19
Juncus conglomeratus	0	0
Lonicera periclymenum	2.44	2.44
Luzula pilosa	0	0
Luzula sylvatica	10.03	10.03
Lycopodium spp.	1.31	1.28
Lysimachia nummularia	1.62	1.56
Mercurialis perennis	0	0
Molinia caerulea	9.14	9.08
Nardus stricta	1.27	1.27
Oreopteris limbosperma	1.01	1.01
Oxalis acetosella	6.64	6.80
Plantago lanceolata	3.18	3.12
Poa annua	0	0
Poa nemoralis	0	0
Polygala serpyllifolia	0.20	0.20
Potentilla erecta	6.74	7.04
Primula vulgaris	3.31	3.23
Primular elatidor	0	0
Prunella vulgaris	0.53	0.53

Pteridium aquilinum	44.52	43.58
Quercus spp.	1.84	2.32
Ranunculus acris	2.27	2.27
Ranunculus repens	0.62	0.62
Rosa cania	0.51	0.51
Rubus fruticosus agg.	4.45	4.42
Senecio jacobea	0.60	0.60
Sorbus acuparia	2.74	3.02
Spagnum spp.	47.97	47.92
Succiusa pratensis	7.45	7.45
Taraxacum agg.	0.91	0.94
Teucrium scorodonia	1.40	1.40
Urtica dioica	0	0
Vaccinium myrtillus	15.61	15.61
Vaccinium vitis-idaea	0.00	11.28
Viola riviniana	6.81	6.95
Leaf litter	27.11	26.55
Lichen	0.33	0.33
Rock	1.22	0.78
Soil	10.41	10.41

Note: Species indicative of ***grazed*** woodland indicated in bold, ***un-grazed*** underlined and bold, taken from (McEvoy et al., 2006)

4.3 Aims

The hypothesis that the ecosystem engineering action of grazing by deer, or its absence through exclusion, may affect habitat conditions such as vegetation architecture and botanical species diversity, affecting the availability of resources to invertebrates was tested. The aim was to experimentally examine these effects on species inhabiting both the epigeal and herb layers, which will provide a useful tool with which to examine the impact of anthropogenic management of grazing disturbance on biodiversity. There is a need for information on the effects of woodland management on a range of taxonomic groups, particularly the impacts of red deer grazing in Scottish woodlands for which there are very few empirical studies. The aims of this chapter are:

- To assess the role of fencing to exclude grazing as a red deer management practise, in impacting biodiversity in the Letterewe oak woodland.
- To determine the factors affecting the variation in invertebrate biodiversity in the Letterewe oak woodland.
- To make recommendations for planning and management of the woodland to maintain and enhance biodiversity.

The hypotheses that invertebrate community assemblages (1) do not vary between grazed and un-grazed woodland plots, and (2) show no association with habitat variables were tested. By identifying the primary components that determine invertebrate communities in the Letterewe oak woodland, it will be possible to assess the consequences of management practises and to develop grazing policy for biodiversity maintenance in red deer habitats.

4.4 Materials and methods

For details of general methods regarding invertebrate and habitat sampling see Chapter Two. For practical reasons species level identification of Coleoptera was limited to include all groups excluding the Staphylinidae.

4.4.1 Statistical analysis

Statistical analyses were performed using the software R 2.10.1 for Windows (R Development Core Team, 2010) following established techniques (Sokal and Rohlf, 1995, Crawley, 2007). To test the null hypotheses that Coleoptera, syrphid and parasitoid assemblage characteristics showed no response to grazing treatment or other habitat

variation, Generalised Linear Models (GLM's) were used. Analysis of abundance data were performed using GLM's with a Poisson error structure, appropriate for count data, or quasipoisson where there was over dispersion in the response, as was typical. Species richness and diversity measures were analysed using GLM's with a normal error structure. To compare differences in vegetation between grazing treatments *t* tests were used. The distribution of residuals for non-count data was examined graphically to check for normality, and either log or square root transformed as appropriate. Initially all explanatory variables (table 4.2) and quadratic terms for continuous variables were fitted individually to test for significance, and graphical inspection used to look for curvature in the response. Tree models were used to obtain a preliminary ranking of the importance of the explanatory variables in order to distinguish those that best explained the variation in the data, and these were used for initial parameterisation of GLM's. A top down model of all explanatory terms was then fitted to the data including interaction terms, limited to two-way terms, as far as replication in the data would allow. The least significant, highest order interactions were removed sequentially until all remaining terms were significant at $P < 0.05$ to produce the minimal adequate model (MAM). All MAM's were checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity, and the ordered residuals against the normal scores to look for evidence of non-normality of errors. Where heteroscedasticity occurred the response variable was transformed and goodness of fit reassessed. Models were compared using ANOVA to justify retaining or excluding variables, and Akaike's information criterion (AIC) used to compare model fit for models with a normal or Poisson error structure. Where the ANOVA indicated no significant difference between the models ($P > 0.05$) the model with the highest degrees of freedom was retained. Where a significant difference occurred the model with the lowest residual deviance was retained. To plot graphical representations of significant interactions, linear models were used to determine the threshold value above and below which splitting the variable the difference between models was most significant. Lines fitted are either regression lines, or fitted using the predict function in R which uses information from the fitted model to produce a smooth function with which to plot the model from the data.

Table 4. 2 Explanatory variables used in the analysis of Coleoptera, syrphid and parasitoid responses to grazing and habitat variables.

Variable	Invertebrate response			
	Coleoptera	Carabidae	Syrphidae	Parasitica
Grazing	*	*	*	*
Plot size				
Plot age				
Deer density				
Tree/shrub species richness	*	*	*	*
Tree/shrub diversity	*	*	*	*
Tree species richness	*	*	*	*
Tree species diversity	*	*	*	*
Herb species richness	*	*	*	*
Herb species diversity	*	*	*	*
Flowering plant species richness			*	*
Flowering plant diversity			*	
Flowering plant cover			*	
Vascular plant species richness	*	*	*	*
Vascular plant diversity	*	*	*	*
Grass-herb species ratio			*	*
Plant height structural diversity	*	*	*	*
Plant species structural diversity	*	*	*	*
Grass/herb/shrub alpha	*	*	*	*
Canopy cover	*	*	*	*
NVC community	*	*	*	*
Sampling period				*
Bracken cover	*	*	*	*

Note: See Chapter Two for a detailed explanation of each variable. Asterisks indicate inclusion of explanatory variables in the analysis of each invertebrate response.

4.5 Results

4.5.1 Pitfall traps

Pitfall traps captured a total of 21,733 individual Coleoptera (excluding Staphylinidae), which were identified as belonging to 60 species, and 2630 Isopoda belonging to 3 species. In addition traps captured 11,193 Staphylinidae, 2218 Diplopoda, 247 Chilopoda, 635 Arenaea, 697 Mollusca, and 927 Acari of the genus Eutrombidium (see table 4.3). In all a total of 40,280 individual epigeal invertebrates were processed.

4.5.2 Malaise traps

The 28 Malaise traps captured a total of 2532 individuals representing 46 species of hoverfly (table 4.4), and 7580 individuals of 41 parasitoid sub-families. One species of note is the parasitoid *Aleiodes nobilis* known in the UK from a few Irish specimens, and a handful of specimens in Scotland, all collected at least 50, and in many cases nearly 100 years ago. The host species is thought to be a noctuid moth in the genus *Autographa*.

Table 4. 3 List of epigeal invertebrate groups and species, their total abundance, and mean abundance in pitfall traps in grazed and un-grazed sample plots.

			Grazed				Un-grazed			
Family	Genus and species	Total	Mean		SE	n	Mean		SE	n
Eutrombidium spp.	Red soil mites	927	4.07	±	1.54	13	3.62	±	2.28	11
Areneae	Spiders	635	2.76	±	1.09	13	2.51	±	0.87	11
Staphylinidae	Rove beetles	11193	50.17	±	9.18	13	42.46	±	10.28	11
Mollusca	Snails	697	2.63	±	1.04	13	3.23	±	1.12	11
Diplopoda	Millipedes	2218	4.65	±	1.67	13	14.66	±	9.50	11
Chilopoda	Centipedes	247	0.68	±	0.31	13	1.44	±	0.56	11
Isopoda	Woodlice	2630	11.56	±	3.66	13	10.25	±	3.48	11
Carabidae	*Abax parallelepipedus*	1862	9.15	±	1.72	13	6.11	±	1.72	11
Dytiscidae	*Agabus guttatus*	1	0.01	±	0.01	13	0.00	±	0.00	11
Elateridae	*Agriotes obscurus*	57	0.21	±	0.18	13	0.27	±	0.22	11
Carabidae	*Amara communis*	9	0.07	±	0.07	13	0.00	±	0.00	11
Carabidae	*Amara lunicollis*	1	0.01	±	0.01	13	0.00	±	0.00	11
Scarabidae	*Aphodius rufipes*	1	0.01	±	0.01	13	0.00	±	0.00	11
Elateridae	*Athous haemorrhoidalis*	22	0.14	±	0.08	13	0.04	±	0.04	11
Curculionidae	*Barynotus squamosus*	4	0.03	±	0.02	13	0.00	±	0.00	11
Byrrhidae	*Burrhus pilula*	1	0.00	±	0.00	13	0.01	±	0.01	11
Carabidae	*Calathus micropterus*	1	0.01	±	0.01	13	0.00	±	0.00	11
Carabidae	*Calathus rotundicollis*	23	0.18	±	0.15	13	0.00	±	0.00	11
Cantharidae	*Cantharis nigricans*	2	0.02	±	0.02	13	0.00	±	0.00	11
Cantharidae	*Cantharis paludosa*	14	0.11	±	0.11	13	0.00	±	0.00	11
Carabidae	*Carabus clathratus*	2	0.00	±	0.00	13	0.02	±	0.02	11
Carabidae	*Carabus glabratus*	827	3.24	±	0.62	13	3.69	±	0.84	11
Carabidae	*Carabus granulatus*	57	0.32	±	0.23	13	0.14	±	0.10	11
Carabidae	*Carabus nemoralis*	87	0.63	±	0.17	13	0.05	±	0.02	11
Carabidae	*Carabus problematicus*	92	0.57	±	0.13	13	0.16	±	0.06	11
Carabidae	*Carabus violaceous*	88	0.50	±	0.09	13	0.21	±	0.07	11
Chrysomelidae	*Chrysolina staphylea*	6	0.02	±	0.02	13	0.03	±	0.03	11
Elateridae	*Ctenicera cuprea*	19	0.11	±	0.08	13	0.05	±	0.05	11
Carabidae	*Cychrus caraboides*	220	1.17	±	0.44	13	0.62	±	0.37	11
Elateridae	*Dalopius marginatus*	2	0.02	±	0.01	13	0.00	±	0.00	11
Dascillidae	*Dascillus cervinus*	17	0.11	±	0.03	13	0.03	±	0.03	11
Carabidae	*Dromius quadrimaculatus*	1	0.01	±	0.01	13	0.00	±	0.00	11
Geotrupidae	*Geotrupes stercorarius*	3	0.02	±	0.02	13	0.00	±	0.00	11
Geotrupidae	*Geotrupes stercorosus*	3339	18.48	±	4.22	13	8.51	±	2.90	11
Carabidae	*Harpalus latus*	9	0.06	±	0.03	13	0.01	±	0.01	11
Histeridae	*Hister striola*	2	0.00	±	0.00	13	0.02	±	0.02	11
Elateridae	*Hypnoides riparius*	66	0.49	±	0.41	13	0.02	±	0.02	11
Carabidae	*Leistus fulvibarbis*	5	0.01	±	0.01	13	0.04	±	0.04	11
Carabidae	*Leistus rufecens*	3	0.00	±	0.00	13	0.03	±	0.02	11
Carabidae	*Loricera pilicornis*	2	0.00	±	0.00	13	0.02	±	0.02	11
Histeridae	*Margarinotus neglectus*	2	0.02	±	0.02	13	0.00	±	0.00	11
Histeridae	*Margarinotus striloa*	18	0.02	±	0.01	13	0.15	±	0.15	11
Elateridae	*Melanotus rufipes* agg.	2	0.00	±	0.00	13	0.02	±	0.02	11
Carabidae	*Nebria brevocolis*	2162	15.32	±	7.13	13	1.55	±	0.73	11
Silphidae	*Nicrophorus humator*	2	0.02	±	0.02	13	0.00	±	0.00	11
Silphidae	*Nicrophorus investigator*	2	0.02	±	0.02	13	0.00	±	0.00	11
Silphidae	*Nicrophorus vespilloides*	1109	4.37	±	0.93	13	4.92	±	1.13	11
Silphidae	*Oiceoptoma thoracica*	148	0.84	±	0.27	13	0.35	±	0.24	11

Staphylinidae	*Othius punctatulus*	1	0.01	±	0.01	13	0.00	±	0.00	11
Curculionidae	*Otiorhynchus scaber*	42	0.28	±	0.14	13	0.05	±	0.04	11
Curculionidae	*Otiorhynchus singularis*	39	0.25	±	0.17	13	0.06	±	0.03	11
Curculionidae	*Otiorhynchus sulcatus*	1	0.01	±	0.01	13	0.00	±	0.00	11
Carabidae	*Poecilus cupreus*	138	0.88	±	0.51	13	0.22	±	0.13	11
Elateridae	*Prosternon holosericeus*	65	0.49	±	0.39	13	0.01	±	0.01	11
Carabidae	*Pterostichus diligens*	97	0.55	±	0.23	13	0.24	±	0.12	11
Carabidae	*Pterostichus madidus*	6652	34.68	±	7.19	13	19.49	±	5.12	11
Carabidae	*Pterostichus melanarius*	2719	17.46	±	5.94	13	4.08	±	1.49	11
Carabidae	*Pterostichus niger*	1502	8.58	±	2.54	13	3.51	±	2.04	11
Carabidae	*Pterostichus nigrita*	100	0.62	±	0.31	13	0.18	±	0.09	11
Carabidae	*Pterostichus strenuus*	9	0.03	±	0.02	13	0.05	±	0.05	11
Carabidae	*Rhagonydia femoralis*	1	0.01	±	0.01	13	0.00	±	0.00	11
Elateridae	*Selatosomus impressus*	13	0.10	±	0.05	13	0.00	±	0.00	11
Scarabidae	*Serica brunnea*	20	0.12	±	0.06	13	0.04	±	0.03	11
Silphidae	*Silpha atrata*	22	0.17	±	0.12	13	0.00	±	0.00	11
Silphidae	*Silpha obscura*	9	0.07	±	0.05	13	0.00	±	0.00	11
Curculionidae	*Strophosoma melanogrammum*	12	0.08	±	0.08	13	0.01	±	0.01	11

Table 4. 4 List of hoverfly species, their total abundance in malaise traps, and mean abundance and standard errors in grazed and un-grazed oak woodland sample plots.

			Grazed				Un-grazed			
Family	Genus and species	Total	Mean		SE	n	Mean		SE	n
Bacchini	*Baccha elongata*	16	0	±	0	8	8.00	±	0	6
Xylotini	*Chalcosyrphus nemorum*	9	1.00	±	0	8	1.00	±	0	6
Cheilosiini	*Cheilosia longula*	4	1.00	±	0	8	1.50	±	0	6
Cheilosiini	*Cheilosia scutellata*	1	1.00	±	0	8	0	±	0	6
Syrphini	*Chrysotoxum arcuatum*	31	1.77	±	0.58	8	1.89	±	0.48	6
Syrphini	*Dasysyrphus albostriatus*	3	1.00	±	0	8	1.00	±	0	6
Syrphini	*Dasysyrphus hilaris*	1	1.00	±	0	8	0	±	0	6
Syrphini	*Dasysyrphus pinastri*	1	1.00	±	0	8	0	±	0	6
Syrphini	*Dasysyrphus tricinctus*	7	1.50	±	0.50	8	1.25	±	0.25	6
Syrphini	*Dasysyrphus venustus*	2	2.00	±	0	8	0	±	0	6
Syrphini	*Didea fasciata*	1	1.00	±	0	8	0	±	0	6
Syrphini	*Epistrophe grossulariae*	14	3.50	±	2.50	8	1.33	±	0.33	6
Syrphini	*Episyrphus balteatus*	220	4.13	±	0.96	8	3.29	±	0.77	6
Eristalini	*Eristalis pertinax*	1	1.00	±	0	8	0	±	0	6
Syrphini	*Eupeodes corollae*	18	1.50	±	0.50	8	1.00	±	0	6
Syrphini	*Eupeodes lundbecki*	1	1.00	±	0	8	0	±	0	6
Syrphini	*Eupeodes luniger*	1	1.00	±	0	8	0	±	0	6
Cheilosiini	*Ferdinandea cuprea*	1	1.00	±	0	8	0	±	0	6
Syrphini	*Melangyna cincta*	2	0	±	0	8	1.00	±	0	6
Syrphini	*Melangyna lasiophthalma*	92	4.35	±	1.74	8	2.13	±	0.29	6
Bacchini	*Melanostoma mellinum*	38	2.36	±	0.35	8	1.73	±	0.45	6
Bacchini	*Melanostoma scalare*	1056	10.03	±	1.54	8	12.41	±	2.47	6
Bacchini	*Melanostoma sp*	10	1.33	±	0.33	8	1.33	±	0.33	6
Syrphini	*Meliscaeva auricollis*	21	1.43	±	0.17	8	1.13	±	0.13	6
Syrphini	*Meliscaeva cinctella*	60	1.63	±	0.25	8	1.75	±	0.47	6
Eristalini	*Myathropa florea*	78	2.10	±	0.39	8	1.78	±	0.26	6
Syrphini	*Parasyrphus punctulatus*	2	1.00	±	0.00	8	0	±	0	6
Bacchini	*Platycheirus albimanus*	192	2.31	±	0.37	8	2.77	±	0.57	6
Bacchini	*Platycheirus nielseni*	31	2.10	±	0.46	8	1.61	±	0.29	6
Bacchini	*Platycheirus peltatus*	2	1.00	±	0	8	1.00	±	0	6
Bacchini	*Platycheirus scutatus*	4	1.00	±	0	8	1.00	±	0	6
Bacchini	*Platycheirus scutatus sl*	8	1.25	±	0.25	8	1.00	±	0	6
Bacchini	*Platycheirus sp*	6	1.00	±	0	8	0	±	0	6
Cheilosiini	*Rhingia campestris*	1	0	±	0	8	1.25	±	0.25	6
Pipizini	*Sericomyia lappona*	1	0	±	0	8	1.00	±	0	6
Pipizini	*Sericomyia silentis*	34	0	±	0	8	1.00	±	0	6
Syrphini	*Sphaerophoria sp*	4	1.38	±	0.20	8	1.20	±	0.12	6
Chrysogastrini	*Sphegina clunipes*	27	0	±	0	8	1.00	±	0	6
Syrphini	*Syrphus ribesii*	137	1.25	±	0.25	8	3.67	±	2.67	6
Syrphini	*Syrphus sp*	9	2.69	±	0.57	8	2.83	±	0.67	6
Syrphini	*Syrphus torvus*	108	1.75	±	0.48	8	2.00	±	0	6
Syrphini	*Syrphus vitripennis*	162	2.53	±	0.39	8	1.84	±	0.42	6
Bacchini	*Xanthandrus comtus*	1	2.65	±	0.51	8	2.61	±	0.46	6
Xylotini	*Xylota jakutorum*	1	0	±	0	8	1.00	±	0	6
Xylotini	*Xylota segnis*	1	0	±	0	8	0.50	±	0.50	6

4.5.3 Species accumulation

Species accumulation curves (figure 4.1) were plotted to illustrate the rate at which new species were trapped, with each data set as a whole, and for traps in grazed and un-grazed plots, to determine the efficacy of the sampling effort, and indicate the extent to which the woodland fauna was sampled. Random permutations and sub-sampling of the data without replacement were used to find the mean and its standard deviation. The cumulative number of species recorded (S) is plotted as a function of sampling effort (n). For malaise traps, a variance components analysis revealed most variation at the level of individual malaise trap, which is therefore used as the measure of sampling effort. Curves were generated by running 28 (all traps) 16 (traps in grazed plots) or 12 (traps in fenced plots) sequences of accumulations, one with each of the traps at the start, and then adding one trap at random until all traps were used. For pitfall traps, curves were generated by running 10 (the number of pitfall traps per sample plot) sequences of accumulations for each grazed and un-grazed plot per year, and 100 (2007) and 130 (2008) sequences of accumulations for all traps per year, again adding one trap at random until all traps were used. Graphical inspection revealed that the curves for both hoverflies and beetles did not reach obvious asymptotes, however the rate of accumulation of new species with increased sampling effort had levelled off sufficiently, such that sampling effort was considered satisfactory. Hoverfly species accumulated more rapidly in un-grazed plots, while beetle species accumulated more rapidly in grazed plots.

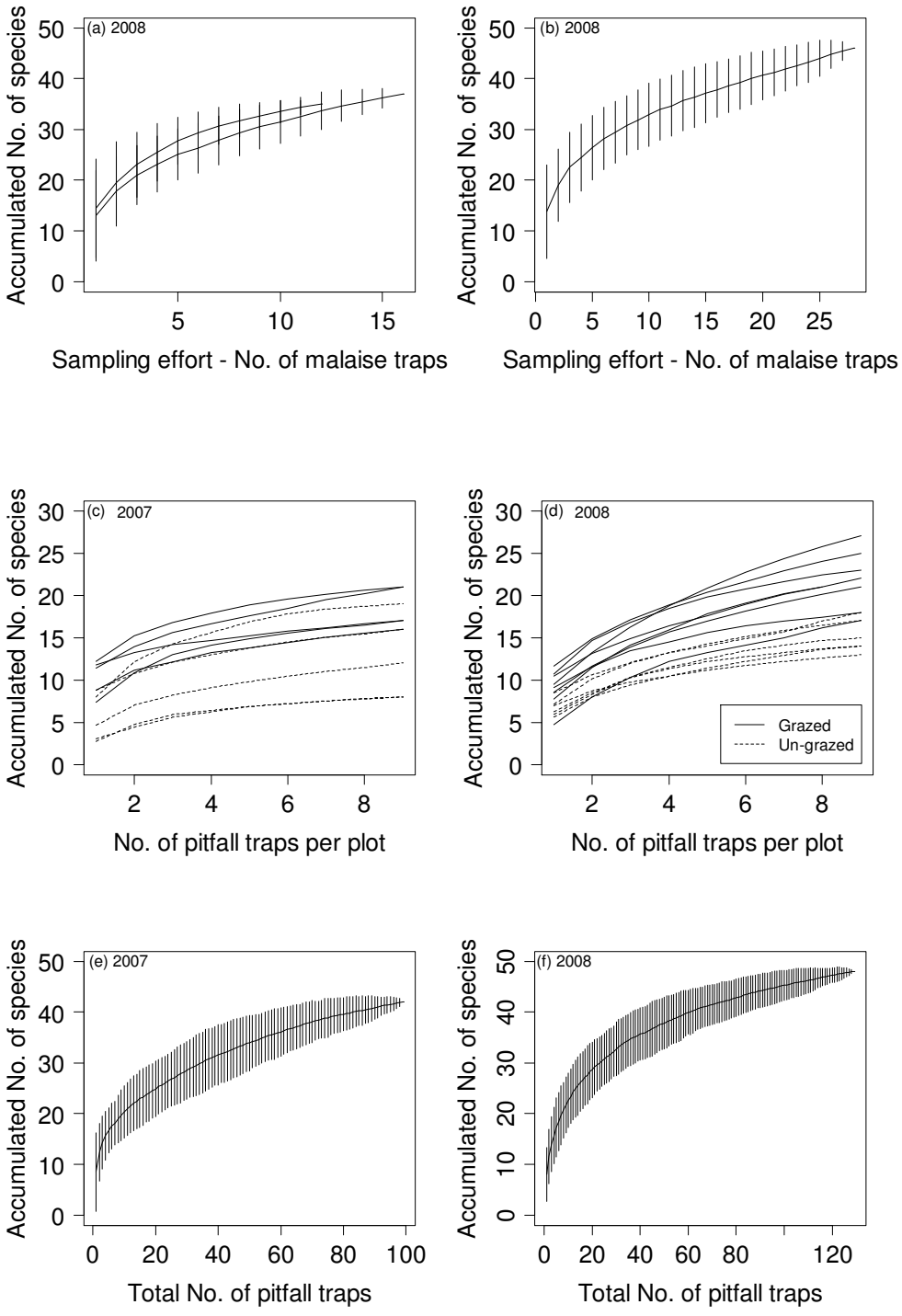


Figure 4. 1 Species accumulation curves for hoverflies in (a) grazed/un-grazed plots, (b) all plots combined, beetles species in grazed and un-grazed plots in (c) 2007 and (d) 2008, and all plots combined in (e) (2007) and (f) 2008.

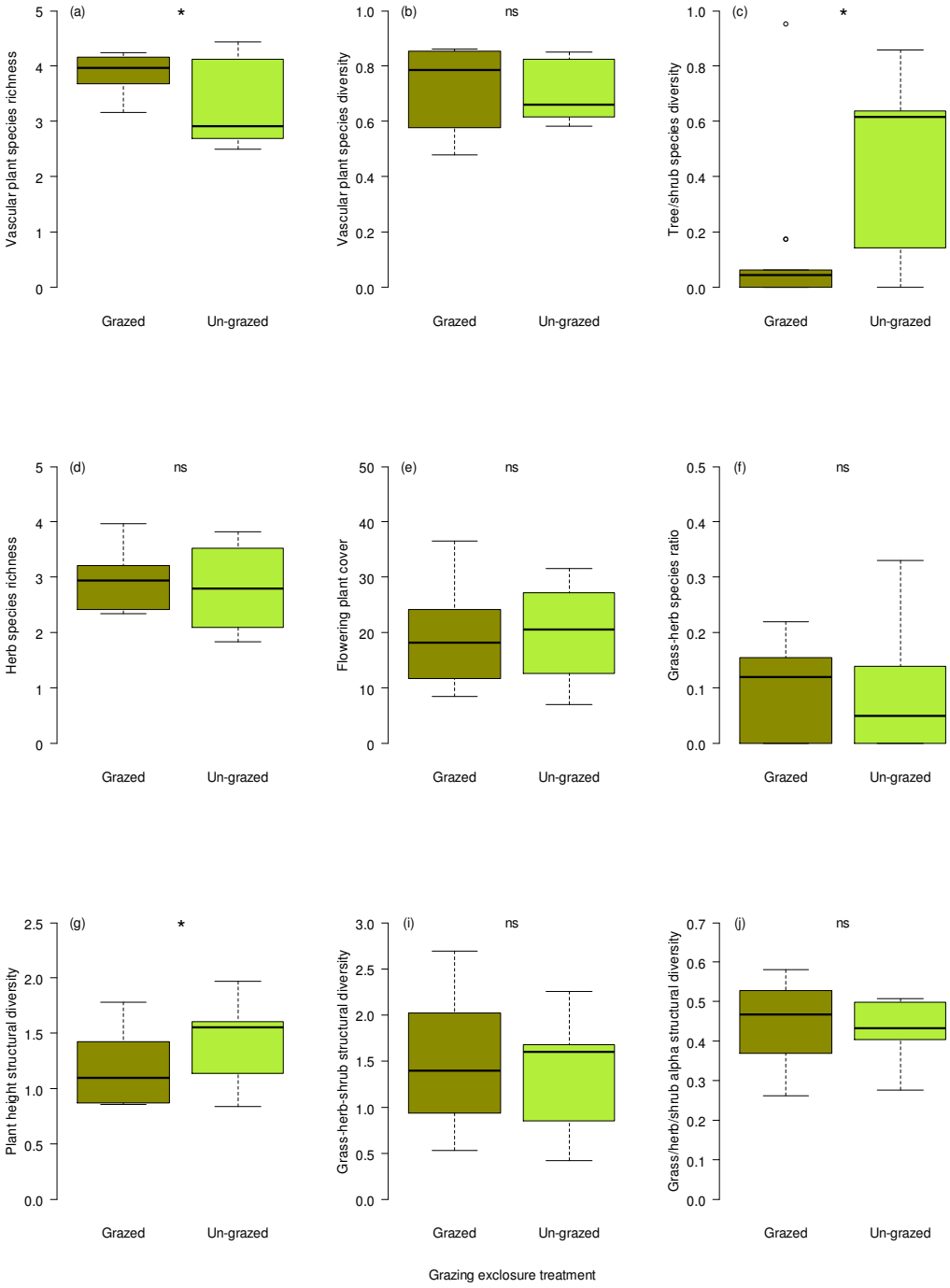


Figure 4. 2 Boxplots illustrating differences in vegetation characteristics between grazed and un-grazed treatment plots in the Letterewe oak woodland. (a) Vascular plant species richness (b) Vascular plant species diversity, (c) Tree/shrub species richness, (d) Herb species richness, (e) Flowering plant cover, (f) grass-herb species ratio, (g) Plant height structural diversity, (h) Plant species structural diversity and (i) Grass/herb/shrub alpha structural diversity. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002). Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***. Non-significant effects are indicated by 'ns'. For statistics see table 4.5, n = 14.

Table 4. 5 Differences in vegetation characteristics between grazed and un-grazed treatment plots in 2008 in the Letterewe oak woodland. t value: model t statistic. *P*: model P value. df: degrees of freedom.

	Mean					
Vegetation variable	Grazed	Un-grazed	*t*	df	*P*	
Vascular plant species richness	3.863	3.316	2.284	22	0.032	*
Vascular plant species diversity	0.718	0.711	0.119	22	0.906	ns
Tree/shrub species diversity	0.120	0.437	-2.652	22	0.015	*
Herb species richness	2.931	2.810	1.087	22	0.279	ns
Flowering plant cover	19.155	19.935	-0.490	22	0.625	ns
Grass-herb species ratio	0.096	0.095	0.070	22	0.945	ns
Plant height structural diversity	1.233	1.376	-2.186	22	0.031	*
Plant species structural diversity	1.544	1.420	0.454	22	0.654	ns
Grass/herb/shrub alpha structural diversity	0.452	0.434	0.519	22	0.609	ns

Notes: Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***. Non-significant effects are indicated by 'ns', n = 24.

4.5.4 Grazing effects

Total Coleoptera abundance (figure 4.3a), Coleoptera species richness (figure 4.3b), and carabid abundance (figure 4.4a) were significantly higher in grazed than in un-grazed plots. There was no difference in Coleoptera species diversity (figure 4.3c), carabid species richness (figure 4.3c) or carabid species diversity (figure 4.4c) between grazed and un-grazed plots. Hoverflies were significantly more abundant in grazed than in un-grazed plots (figure 4.11a), while the abundance of the three most common hoverfly species (figure 4.12a-c), hoverfly species richness (figure 4.11b), hoverfly species diversity (figure figure 4.11c), and parasitoid abundance (figure 4.23a) did not differ between grazed and un-grazed plots. There was no instance of an invertebrate response having a lower value in un-grazed than in grazed plots.

4.5.5 Effects of other habitat variables

The only significant predictor of Coleoptera abundance other than grazing was canopy cover, with which there was a positive correlation (figure figure 4.5a). Coleoptera species richness was predicted by year (figure 4.5b), and tree species richness (figure 4.5c), in

addition to grazing. The year effect resulted in more species recorded in 2008 than in 2007, and there was a positive relationship with tree species richness. Coleoptera species diversity was predicted by bryophyte cover (figure 4.5d), which caused a decline, and the interaction between vascular plant species richness with tree species diversity (figure 4.6). Low vascular plant species richness elicited a steep rise in Coleoptera species diversity, while at high levels of vascular plant species richness there is an almost imperceptible decline. In addition to grazing, the only other significant predictor of carabid abundance was the interaction between year and NVC community (figure 4.8), carabids more abundant in 2007 than in 2008, and most abundant in W11c and least abundant in W11b in 2007, while in 2008 they were most abundant in W17a and least so in W11c. Carabid species richness declined in response to leaf litter cover (figure 4.7), it's sole significant predictor, while a more complex set of two two-way interactions explained the response of carabid species diversity. At low levels of vegetation structural diversity, carabid species diversity was positively correlated with vascular plant species richness and at high levels of vegetation structural diversity negatively so (figure 4.9). The year effect interacting with vegetation structural diversity caused a decline in carabid species richness in 2007 and an increase in 2008 (figure 4.10).

Hoverfly abundance was significantly predicted by structural diversity of vegetation, implied by a plant type gradient (figure 4.13a), and the interaction between tree/shrub species richness and grazing (figure 4.14). Abundance increased in response to structural diversity, and in response to tree/shrub species richness in grazed plots, and declined with richness in un-grazed plots. The abundance of *Melanostoma scalare* was predicted by structural diversity of vegetation, implied by a plant species gradient (figure 4.13b), and the interaction between herb species diversity and flowering plant cover (figure 4.15). Abundance increased in response to structural diversity, increased sharply in response to herb species at the lower end of the observed flowering plant percentage cover range, and declined sharply at the upper end. The abundance of *Episyrphus balteatus* was predicted solely by canopy cover (figure 4.16), and showed a positive correlation. *Platycheirus albimanus* abundance was positively correlated with plant height structural diversity (figure 4.17), and with herb species richness at the lower end of the grass-herb species ratio range (figure 4.18).

Continued on page 119

Table 4. 6 Non-significant effects of grazing on invertebrate abundance, richness and diversity in the Letterewe oak woodland. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Response	Estimate	SE	*t* value	*P*		Res. Dev.	df
Coleoptera species diversity							
Intercept	0.763	0.032	24.040	< 0.001	***	40.668	22
Grazing (un-grazed)	-0.038	0.047	-0.802	0.431	ns		
Carabid species richness							
Intercept	0.766	0.056	13.679	< 0.001	***	0.897	22
Grazing (un-grazed)	0.060	0.083	0.728	0.474	ns		
Carabid species diversity							
Intercept	0.475	0.045	10.570	< 0.001	***	0.577	22
Grazing (un-grazed)	-0.006	0.066	-0.097	0.924	ns		
***Melanostoma scalare* abundance**							
Intercept	11.516	0.171	67.445	< 0.001	***	287427	12
Grazing (un-grazed)	0.213	0.246	0.863	0.405	ns		
***Episyrphus balteatus* abundance**							
Intercept	10.629	0.212	50.091	0.000	***	200118	12
Grazing (un-grazed)	-0.226	0.347	-0.653	0.526	ns		
***Platycheirus albimanus* abundance**							
Intercept	10.047	0.175	57.492	< 0.001	***	67067	12
Grazing (un-grazed)	0.184	0.254	0.725	0.482	ns		
Hoverfly species richness							
Intercept	1.731	0.121	14.322	< 0.001	***	1.403	12
Grazing (un-grazed)	0.169	0.185	0.916	0.378	ns		
Hoverfly species diversity							
Intercept	0.696	0.029	24.144	< 0.001	***	0.08	12
Grazing (un-grazed)	-0.001	0.044	-0.028	0.978	ns		
Parasitoid abundance							
Intercept	2.986	0.145	20.562	< 0.001	***	40.668	12
Grazing (un-grazed)	0.102	0.216	0.473	0.645	ns		

Notes: Asterisks indicate the level of significance: *P < 0.05 = *, P < 0.01 = **, P < 0.001 = ****. Non-significant effects are indicated by 'ns'. *P* values for significant effects are taken from the model output of the MAM in each case, non-significant results are the deletion *P* values from the relevant model simplification.

Table 4. 7 Epigeal Coleoptera abundance, richness and diversity in the Letterewe oak woodland: effect sizes and their standard errors of significant explanatory variables. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Invertebrate response	Estimate	SE	*t* value	*P*		Res. Dev.	df
Coleoptera abundance							
Intercept	6.325	0.353	17.9	< 0.001	***	6081.3	21
Canopy cover	0.011	0.004	2.484	0.022	*		
Grazing	-0.667	0.258	-2.583	0.017	*		
Coleoptera species richness (Margalef)							
Intercept	-365.982	98.201	-3.727	0.001	**	0.278	20
Grazing	-0.285	0.052	-5.471	< 0.001	***		
Year	0.183	0.049	3.744	0.001	**		
Tree species richness	0.132	0.041	3.198	0.005	**		
Coleoptera species diversity (Simpson's D)							
Intercept	0.324	0.114	2.834	0.011	*	0.064	19
Bryophyte cover	-0.004	0.001	-5.805	< 0.001	***		
Tree species diversity	1.540	0.265	5.813	< 0.001	***		
Vascular plant species richness	0.147	0.030	4.873	< 0.001	***		
Tree species diversity : vascular plant species richness	-0.387	0.069	-5.607	< 0.001	***		
Carabid abundance							
Intercept	-1634.155	1263.624	-1.293	0.213		2603.2	17
Grazing	-0.716	0.223	-3.204	0.005	**		
Year	0.817	0.629	1.298	0.212			
NVC W17a	2269.561	1379.784	1.645	0.118			
NVC W17c	4500.267	1633.222	2.755	0.014	*		
Year : NVC W17a	-1.130	0.687	-1.644	0.119			
Year : NVC W17c	-2.241	0.814	-2.755	0.014	*		
Carabid species richness							
Intercept	0.893	0.061	14.589	< 0.001	***	0.768	22
Leaf litter cover	-0.005	0.003	-2.077	0.050	*		
Carabid species diversity							
Intercept	636.263	278.913	2.281	0.035	*	0.153	18
Plant species richness	0.503	0.132	3.818	0.001	**		
Year	-0.318	0.139	-2.287	0.035	*		
Vegetation structural diversity	-595.244	203.723	-2.922	0.009	**		
Vegetation species richness : vegetation structural diversity	-0.376	0.097	-3.890	0.001	**		
Year : vegetation structural diversity	0.297	0.101	2.930	0.009	**		

Notes: Minimal adequate models for epigeal (a) Coleoptera abundance as a function of canopy cover and grazing. Explanatory variables excluded during model simplification included canopy cover : bryophyte over *(P = 0.829)*, bryophyte cover *(P = 0.084)*, canopy cover : grazing *(P = 0.566)*, grazing : year *(P = 0.107)*, year *(P = 0.051)*, canopy cover : tree species richness *(P = 0.176)*, grazing : tree species richness *(P = 0.325)*, tree species richness *(P = 0.260)*, canopy cover : vascular plant species richness *(P = 0.348)*, grazing : vascular plant species richness *(P = 0.230)*, vascular plant species richness *(P = 0.219)*, grazing : vascular plant species diversity *(P = 0.838)*, canopy cover : vascular plant species diversity *(P = 0.201)*, vascular plant species diversity *(P = 0.341)*, grazing : vegetation structural complexity *(P = 0.879)*, canopy cover : vegetation structural complexity *(P = 0.837)*, vegetation structural complexity *(P = 0.716)*, grazing : plant species structure *(P = 0.980)*, canopy cover : plant species structure *(P = 0.971)*, plant species structure *(P = 0.278)*, canopy cover : grass/herb/shrub alpha *(P = 0.463)*, grazing : grass/herb/shrub alpha *(P = 0.197)*,

grass/herb/shrub alpha *(P = 0.261)*, grazing : NVC community *(P = 0.749)*, canopy cover : NVC community *(P = 0.104)*, NVC community *(P = 0.381)*, grazing : bracken cover *(P = 0.287)*, canopy cover : bracken cover *(P = 0.298)*, bracken cover *(P = 0.657)*, grazing : leaf litter cover *(P = 0.702)*, canopy cover : leaf litter cover *(P = 0.322)*, leaf litter cover *(P = 0.810)*. (b) Coleoptera species richness as a function of grazing, year and tree species richness, (c) Coleoptera species diversity as a function of bryophyte cover, and tree species diversity : vascular plant species richness, (d) Carabid abundance as a function of grazing, and year : NVC community, (e) Carabid species richness as a function of leaf litter cover, (f) Carabid species diversity as a function of vascular plant species richness : vegetation structural diversity and year : vegetation structural diversity. Model simplification for all models follows the same protocol as (a). See Chapter Two for a full explanation of each of the explanatory variables. Models of abundance data are Generalized Linear Models with a quasi-Poisson error structure, richness and diversity indices are Linear Models with normal errors. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance. Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***.

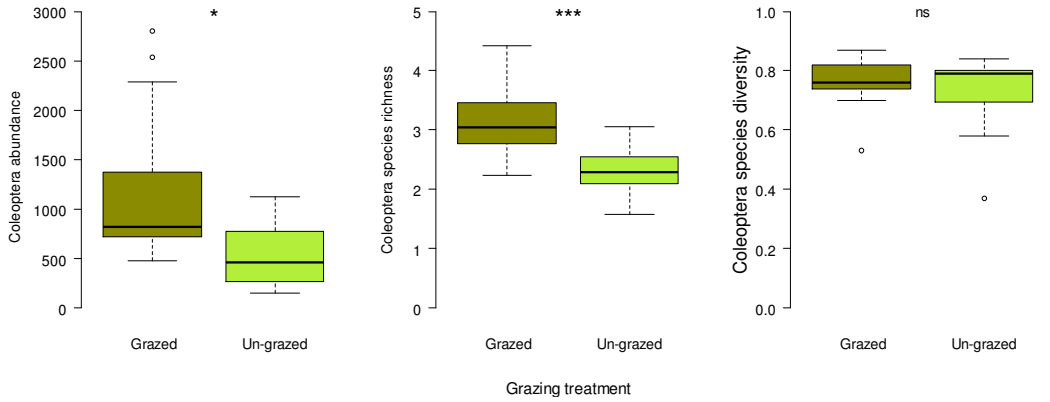


Figure 4. 3 The response to grazing treatment of (a) Coleoptera abundance, (b) Coleoptera species richness, and (c) Coleoptera species diversity. Significant differences in the abundance and species richness but not diversity were detected between grazed and un-grazed treatments in the generalised linear models for Coleoptera. Coleoptera were more abundant (a) Estimate (Grazed) = 6.325, (Un-grazed) = 5.658, SE = 0.258, *t* value = -2.583, *P* = 0.017, df = 21, (GLM with quasipoisson errors) and more species rich (b) Estimate (Grazed) = -365.982 (Un-grazed) = 365.697, SE = 0.052, *t* value = -5.471, *P* = < 0.001, df = 20, (GLM, response variable square root transformed) but did not vary in diversity (c) Estimate (Grazed) = 0.763 (Un-grazed) = 0.725, SE = 0.047, *t* value = -0.802, *P* = 0.431, df = 22, (GLM with normal errors) between grazed and un-grazed treatments. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 4.6. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 24.

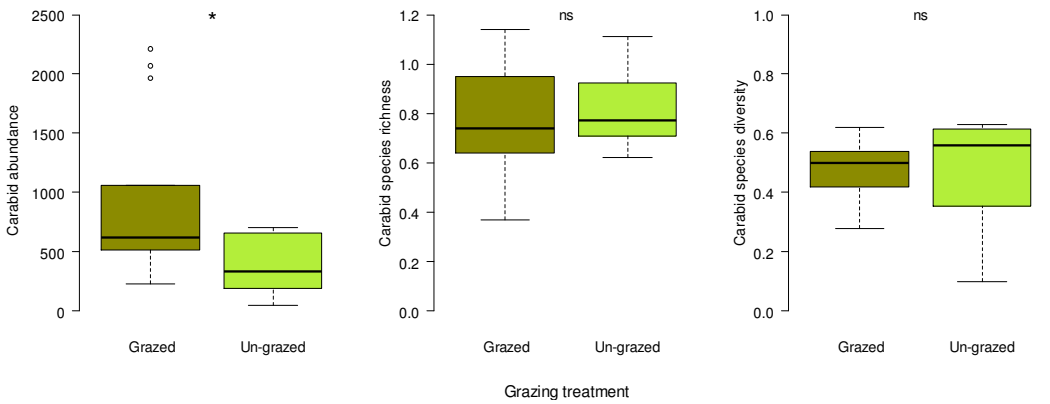


Figure 4. 4 The response to grazing treatment of (a) Carabid abundance, (b) Carabid species richness, and (c) Carabid species diversity. A significant difference in the abundance, but not species richness or diversity, were detected in the generalised linear models for carabids. Abundance was higher in grazed (a) Estimate (Grazed) = -1634.155, (Un-grazed) = -1634.871, SE = 1263.624, *t* value = -1.293, *P* = 0.213, df = 17, (GLM with quasipoisson error structure) and richness (b) Estimate (Grazed) = 0.766, (Un-grazed) = 0.706, SE = 0.083, *t* value = 0.728, *P* = 0.474, df = 22, (GLM with normal errors) and diversity (c) Estimate (Grazed) = 0.475, (Un-grazed) = 0.469, SE = 0.066, *t* value = -0.097, *P* = 0.924, df = 22, (GLM with normal errors) did not vary, between grazed and un-grazed treatments. Boxes show the interquartile range with the median shown as a bold line. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 4.6. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 24.

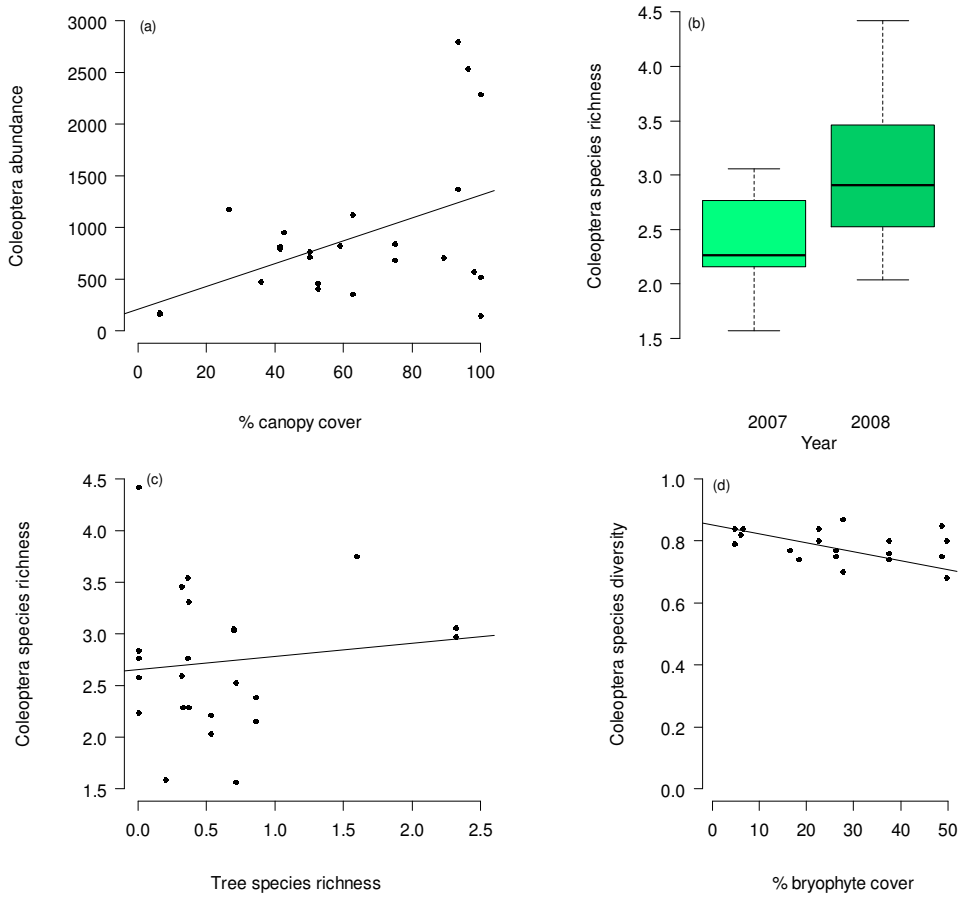


Figure 4. 5 The response of (a) Coleoptera abundance to percentage canopy cover, Coleoptera species richness to (b) year, (c) tree species richness and Coleoptera species diversity to (d) bryophyte cover. Significant effects of (a) percentage canopy cover, (b) year and (c) tree species richness (Margalef's D), and (d) percentage bryophyte cover were detected in the generalised linear models for Coleoptera abundance, Coleoptera species richness, and Coleoptera species diversity respectively. Coleoptera abundance increased in response to increasing percentage canopy cover (Estimate = 0.011, SE = 0.004, *t* value = 2.484, *P* = 0.022, df = 21), Coleoptera were more species rich in 2008 than in 2007 (Estimate = 0.183, SE = 0.049, *t* value = 3.744, *P* = 0.001, df = 20), Coleoptera species richness increased in response to tree species richness (Estimate = 0.132, SE = 0.041, *t* value = 3.198, *P* = 0.005, df = 20), and Coleoptera species diversity declined in response to increasing bryophyte cover (Estimate = -0.004, SE = 0.001, *t* value = -5.805, *P* = < 0.001, df = 19). Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002). Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 4.6. Lines drawn are regressions of the relationships between the variables, n = 24.

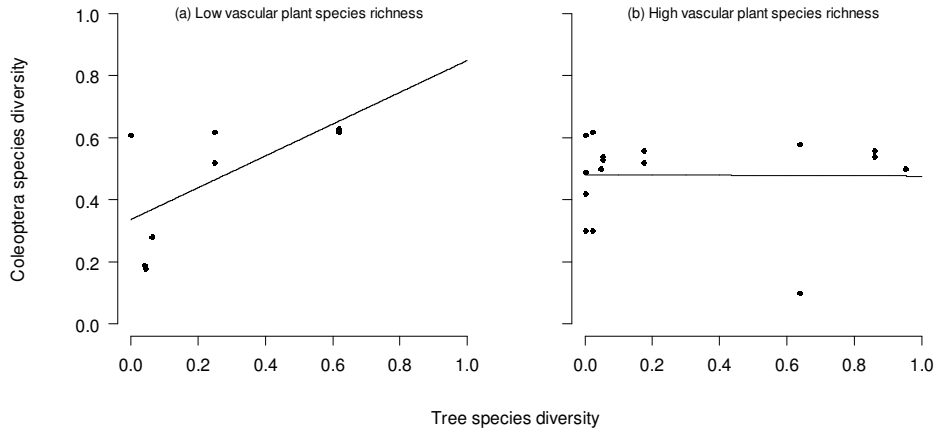


Figure 4. 6 The response of Coleoptera species diversity to the interaction between tree species diversity and vascular plant species richness. A significant effect of the interaction between tree species diversity (Simpson's D) and vascular plant species richness (Margalef' D) was detected in the generalised linear model for Coleoptera species diversity. Where vascular plant species richness was low, Coleoptera species diversity increased with increasing tree species diversity, while not relationship was observed where vascular plant species diversity was high (Estimate = -0.387, SE = 0.069, *t* value = -5.607, *P* = < 0.001, df = 19. Low vascular plant species richness ≤ 3.17, high vascular plant species diversity > 3.17, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.6. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 24.

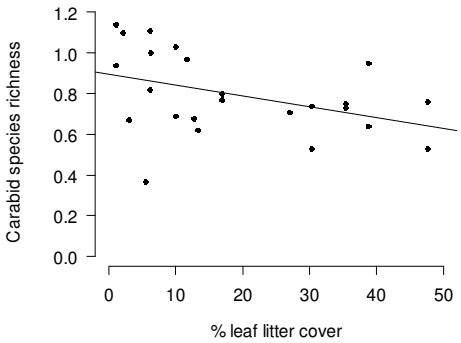


Figure 4. 7 The response of carabid species richness to percentage leaf litter cover. A significant effect of percentage leaf litter cover was detected in the generalised linear model for carabid species richness. Carabid species declined in response to increasing leaf litter cover. Estimate = -0.005, SE = 0.003, *t* value = -2.077, *P* = < 0.05, df = 22. Note that this figure does not take account of all the factors in the minimal adequate model, but is representative of the general underlying relationships shown in table 4.6. Line drawn is the regression fitted from the linear model of the relationship between the variables, n = 24.

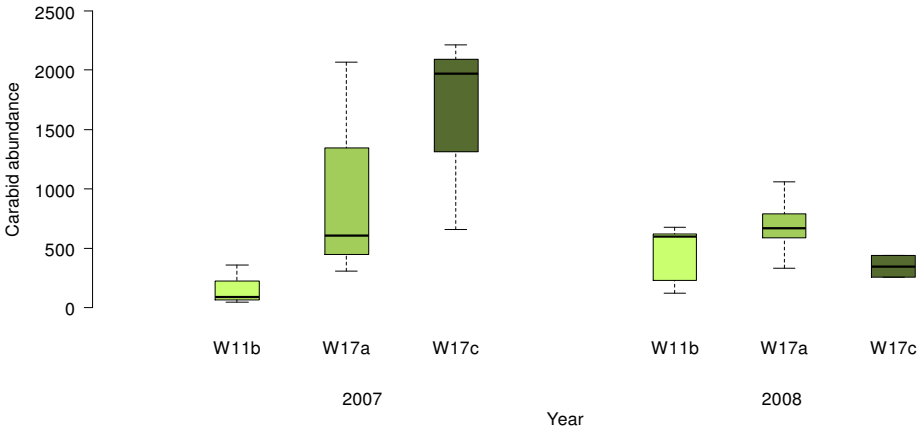


Figure 4. 8 The response of carabid abundance to the interaction between year and NVC community. A significant effect of the interaction between NVC community and year was detected in the generalised linear model for carabid abundance. Carabid abundance ~ year : NVC W17c: Estimate = -2.241, SE = 0.814, *t* value = -2.755, *P* = 0.014, df = 17.Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002). Note that these figures do not take into account all the factors in the full model shown in table 4.6, but are representative of the general underlying relationships. n = 24. NVC communities: W11b *Q. petraea - B. pubescens - Oxalis acetosela, Blechnum spicant* sub-community, W11c *Q. patraea – B. pubescens – Dicranum majus, Isothecium myosuroides – Diplophylum albicans* sub-community, W17a *Q. petraea – B. pubescens – Dicranum majus, Anthoxanthum odoratum – Agrostis capillaris* sub-community.

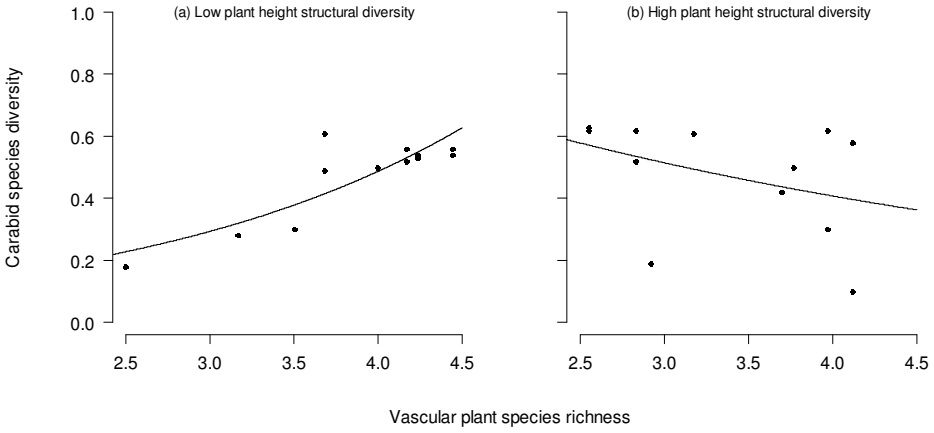


Figure 4. 9 The response of carabid species diversity to the interaction between vascular plant species richness and vegetation height structural diversity. A significant effect of the interaction between plant height structural diversity (alpha diversity index) and vascular plant species richness (Margalef' D) was detected in the generalised linear model for carabid species diversity. Where vascular plant height structural diversity was low, carabid species diversity increased with increasing vascular plant species richness, and declined where plant height structural diversity was high Estimate = -0.376, SE = 0.097, *t* value = -3.890, *P* = 0.001, df = 18.. Low plant height structural diversity ≤ 1.3, high vascular plant species diversity > 1.3, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.6. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 24.

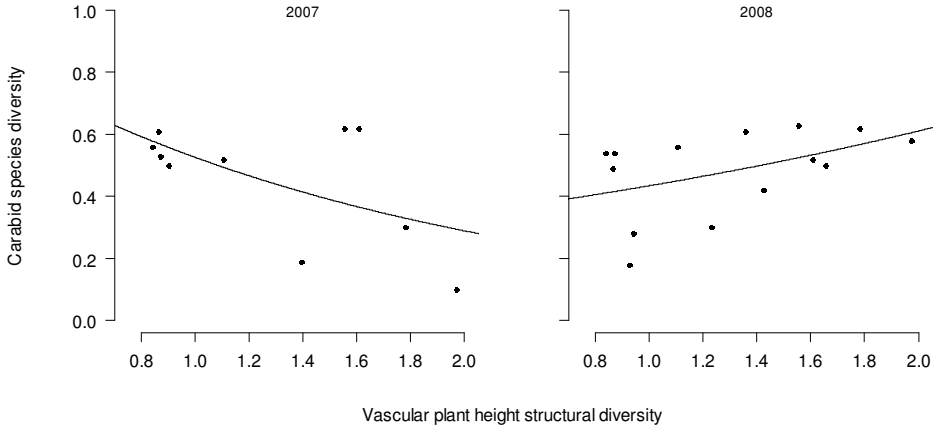


Figure 4. 10 The response of carabid species diversity to the interaction between plant height structural diversity and year (a) 2007 and (b) 2008. A significant effect of the interaction between year and plant height structural diversity was detected in the generalised linear model for carabid species diversity. In 2007 carabid species diversity declined, and in 2008 increased, in response to increasing plant height structural diversity. Estimate = 0.297, SE = 0.101, *t* value = 2.930, *P* = 0.009, df = 19. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.6 Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 24.

Table 4. 8 Syrphid abundance, richness and diversity in the Letterewe oak woodland: effect sizes and their standard errors of significant explanatory variables. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance.

	Estimate	SE	*t* value	*P*		Res. Dev.	df
Hoverfly abundance							
Intercept	8.889	0.314	28.332	< 0.001	***	16409.000	9
Plant species structural diversity	0.477	0.142	3.364	0.008	**		
Tree/shrub species richness	0.506	0.215	2.354	0.004	**		
Grazing	0.673	0.270	2.493	0.043	*		
Tree/shrub species richness : Grazing	-0.766	0.307	-2.497	0.034	*		
***Melanostoma scalare* abundance**							
Intercept	0.976	1.702	0.574	0.580		31151.000	9
Plant species structural diversity	0.317	0.080	3.975	0.003	**		
Herb species diversity	12.101	2.067	5.855	< 0.001	***		
Flowering plant cover	0.480	0.076	6.310	< 0.001	***		
Herb species diversity : flowering plant cover	-0.581	0.096	-6.072	< 0.001	***		
***Episyrphus balteatus* abundance**							
Intercept	9.678	0.425	22.756	< 0.001	***	138097.000	12
Canopy cover	0.013	0.006	2.328	0.038	*		
***Platycheirus albimanus* abundance**							
Intercept	5.219	0.887	5.886	0.001	***	3363.800	7
Grass-herb species ratio	50.138	6.976	7.187	< 0.001	***		
Herb species diversity	4.812	1.017	4.729	0.002	**		
Flowering plant cover	0.023	0.006	3.561	0.009	**		
Vegetation structural diversity	0.490	0.112	4.372	0.003	**		
Grass-herb species ratio : herb species diversity	-57.608	7.967	-7.231	< 0.001	***		
Grass-herb species ratio : flowering plant cover	-0.306	0.054	-5.684	0.001	***		
Hoverfly species richness							
Intercept	4.095	0.764	5.362	< 0.001	***	0.610	10
Grass-herb-shrub alpha	-4.906	1.837	-2.670	0.023	*		
Canopy cover	-0.048	0.013	-3.695	0.004	**		
Grass-herb-shrub alpha : canopy cover	0.101	0.029	3.429	0.006	**		
Hoverfly species diversity							
Intercept	2.367	0.259	9.124	< 0.001	***	0.010	9
Vascular plant species diversity	-2.022	0.362	-5.580	< 0.001	***		
Herb species richness	-0.114	0.023	-5.064	0.001	***		
Grass-herb-shrub alpha	-2.188	0.520	-4.208	0.002	**		
Vascular plant species diversity : grass-herb-shrub alpha	3.332	0.824	4.043	0.003	**		

Notes: Minimal adequate models for (a) Syrphid abundance as a function of plant species structural diversity, and tree/shrub species richness : grazing. Explanatory variables excluded during model simplification included plant species structural diversity : herb species richness *(P = 0.513)*, plant species structural diversity : tree/shrub species richness *(P = 0.116)*, herb species richness : tree/shrub species richness *(P = 0.220)*, herb species richness *(P = 0.980)*, plant species structural diversity : grazing *(P = 0.547)*, tree/shrub

species richness : grazing *(P = 0.877)*, plant species structural diversity : tree/shrub species diversity *(P = 0.572)*, grazing : tree/shrub species diversity *(P = 0.112)*, tree/shrub species richness : tree/shrub species diversity *(P = 0.068)*, tree/shrub species richness *(P = 0.656)*, tree/shrub species richness : grazing *(P = 0.877)*, tree shrub species richness *(P = 0.656)*, plant species structural diversity : tree species diversity *(P = 0.572)*, grazing : tree species diversity *(P = 0.112)*, tree/shrub species richness : tree species diversity *(P = 0.068)*, tree species diversity *(P = 0.323)*, plant species structural diversity : herb species diversity *(P = 0.445)*, grazing : herb species diversity *(P = 0.559)*, herb species diversity *(P = 0.364)*, tree/shrub species richness : flowering plant species richness *(P = 0.878)*, grazing : flowering plant species richness *(P = 0.426)*, flowering plant species richness *(P = 0.834)*, plant species structural diversity : flowering plant species diversity *(P = 0.792)*, flowering plant species diversity *(P = 0.448)*, plant species structural diversity : flowering plant cover *(P = 0.745)*, grazing : flowering plant cover *(P = 0.417)*, tree/shrub species richness : flowering plant cover *(P = 0.520)*, tree/shrub species richness : grazing *(P = 0.054)*, tree shrub species richness : vascular plant species richness *(P = 0.958)*, grazing : vascular plant species richness *(P = 0.934)*, plant species structural diversity : vascular plant species richness *(P = 0.822)*, vascular plant species richness *(P = 0.925)*, plant species structural diversity : vascular plant species diversity *(P = 0.430)*, tree/shrub species richness : vascular plant species diversity *(P = 0.424)*, grazing : vascular plant species diversity *(P = 0.392)*, vascular plant species diversity *(P = 0.412)*, tree/shrub species richness : grass-herb species ratio *(P = 0.316)*, grazing : grass-herb species ratio *(P = 0.236)*, plant species structural diversity : grass-herb species ratio *(P = 0.314)*, grass-herb species ratio *(P = 0.970)*, plant species structural diversity : vegetation height structural diversity *(P = 0.982)*, tree/shrub species richness : vegetation height structural diversity *(P = 0.438)*, grazing : vegetation height structural diversity *(P = 0.060)*, vegetation height structural diversity *(P = 0.157)*, plant species structural diversity : canopy cover *(P = 0.972)*, tree/shrub species richness : canopy cover *(P = 0.558)*, grazing : canopy cover *(P = 0.404)*, canopy cover *(P = 0.262)*. (b) *Melanostoma scalare* abundance as a function of plant species structural diversity, and herb species diversity : flowering plant cover, (c) *Episyrphus balteatus* abundance as a function of canopy cover, (d) *Platycheirus albimanus* abundance as a function of vegetation height structural diversity, grass-herb species ratio : herb species diversity and grass-herb species ratio : flowering plant cover, (e) Syrphid species richness as a function of grass/herb/shrub alpha : canopy cover, and (f) Syrphid species diversity as a function of herb species richness and vascular plant species diversity : grass/herb/shrub alpha. Model simplification procedure for all models follows that of (a). See Chapter Two for a full explanation of each of the explanatory variables. Models of abundance data are Generalized Linear Models with a quasipoisson error structure, richness and diversity indices are Linear Models with normal errors. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance. Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***.

Table 4. 9 Non-significant effects of grazing on syrphid abundance, richness and diversity in the Letterewe oak woodland. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Syrphid response	Estimate	SE	*t*	*P*		Res.Dev.	df
Hoverfly species richness							
Intercept (Grazed)	1.731	0.121	14.322	0	***	1.403	12
Grazing (Un-grazed)	0.169	0.185	0.916	0.378	ns		
Hoverfly species diversity							
Intercept (Grazed)	0.696	0.029	24.144	0	***	0.08	12
Grazing (Un-grazed)	-0.001	0.044	-0.028	0.978	ns		
***Melanostoma* scalare abundance**							
Intercept (Grazed)	10.034	1.817	5.522	0	***	316.97	12
Grazing (Un-grazed)	2.376	2.776	0.856	0.409	ns		
***Episyrphus* balteatus abundance**							
Intercept (Grazed)	4.131	0.849	4.865	0	***	69.222	12
Grazing (Un-grazed)	-0.837	1.297	-0.645	0.531	ns		
***Platycheirus* albimanus abundance**							
Intercept (Grazed)	2.307	0.424	5.446	0	***	48.64	12
Grazing (Un-grazed)	0.466	0.647	0.72	0.485	ns		

Notes: Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***. Non-significant effects are indicated by 'ns'. *P* values for significant effects are taken from the model output of the MAM in each case, non-significant results are the deletion *P* values from the relevant model simplification.

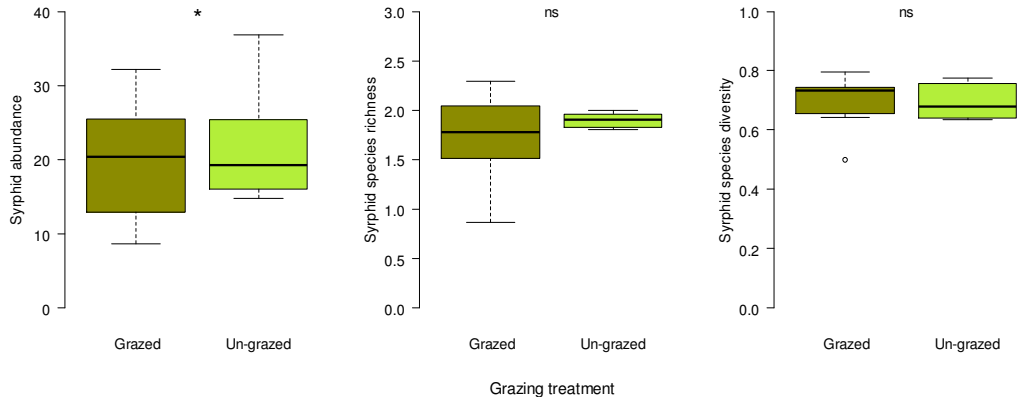


Figure 4. 11 The response of syrphid (a) abundance, (b) species richness and (c) species diversity to grazing. A significant difference in abundance, but no difference in species richness and species diversity were detected in the generalised linear models for Syrphidae. Abundance was higher in grazed than un-grazed (a) Estimate (Grazed) = 8.889, (Un-grazed) = 9.562, SE = 0.270, *t* value = 2.493, *P* = 0.043, df = 9, (GLM with quasipoisson errors) while richness (b) Estimate (Grazed) = 1.731, (Un-grazed) = 1.9, SE = 0.185, *t* value = 0.916, *P* = 0.378, df = 12, (GLM with normal errors) and diversity (c) Estimate (Grazed) = 0.696, (Un-grazed) = 0.694, SE = 0.044, *t* value = -0.028, *P* = 0.978, df = 12, did not vary between grazed and un-grazed treatments. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 4.7. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002). n = 14.

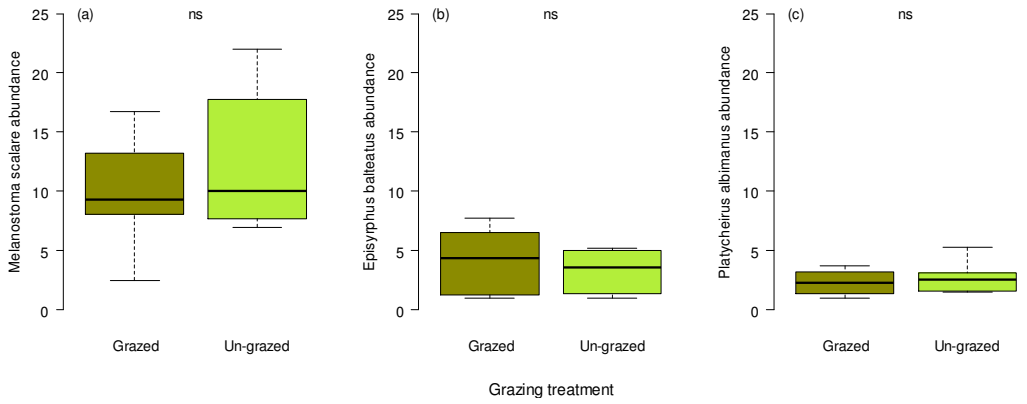


Figure 4. 12 The response of (a) *Melanostoma scalare*, (b) *Episyrphus balteatus* and (c) *Platycheirus albimanus* abundance to grazing. No significant difference in the abundance of *Melanostoma scalare* (a) Estimate (Grazed) = 10.034, (Un-grazed) = 12.41, SE = 2.776, *t* value = 0.856, *P* = 0.409, df = 12, (GLM with normal errors), *Episyrphus balteatus* (b) Estimate (Grazed) = 4.131, (Un-grazed) = 3.295, SE = 1.297, *t* value = -0.645, *P* = 0.531, df = 12, (GLM with normal errors) or *Platycheirus albimanus* (c) Estimate (Grazed) = 2.307, (Un-grazed) = 2.774, SE = 0.647, *t* value = 0.720, *P* = 0.485, df = 12, were detected in the generalised linear models for each species. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 4.7. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002). n = 14.

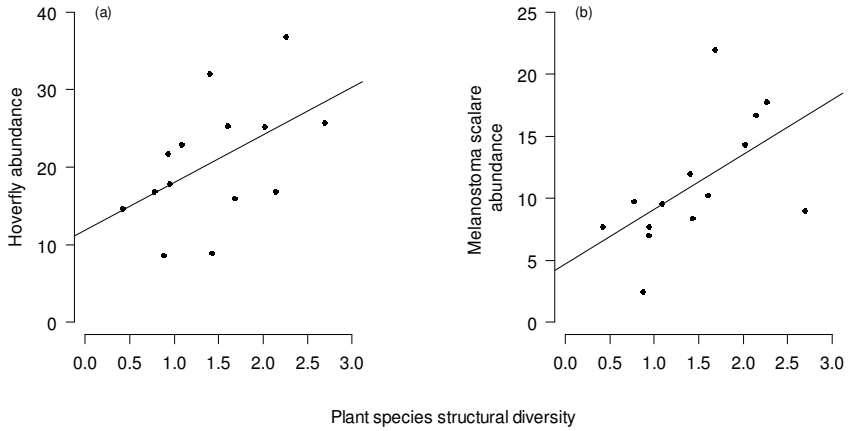


Figure 4. 13 The response of (a) hoverfly abundance and (b) *Melanostoma* scalare to plant species structure diversity. A significant effect of plant species structural diversity was detected in the generalised linear models for (a) hoverfly abundance and (b) *Melanostoma scalare* abundance. In both cases abundance increased in response to increasing plant species structural diversity (a) Estimate = 0.477, SE = 0.142, *t* value = 3.364, *P* = 0.008, df = 9. (b) Estimate = 0317, SE = 0.08, *t* value = 3.975, *P* = 0.003, df = 9. Note that this figure does not take account of all the factors in the minimal adequate model, but is representative of the general underlying relationships shown in table 4.7. Lines drawn are the regressions of the relationships between the variables, n = 14.

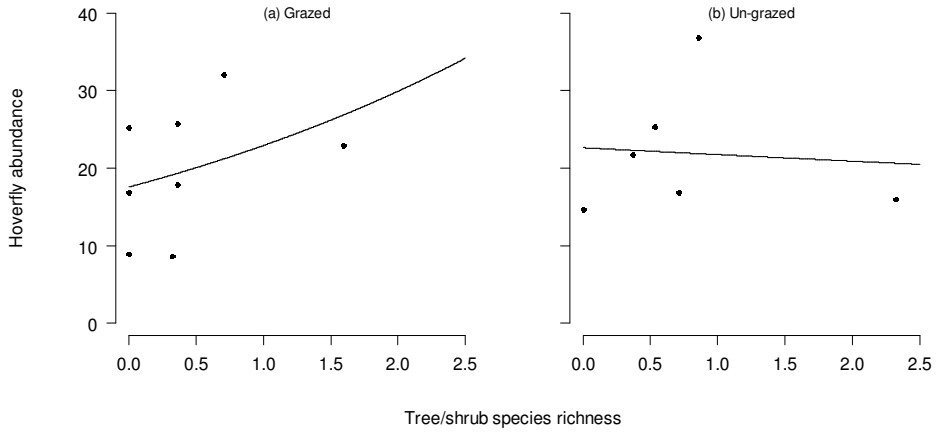


Figure 4. 14 The response of hoverfly abundance to the interaction between grazing and tree/shrub species richness. A significant effect of the interaction between grazing treatment and tree/shrub species richness was detected in the generalised linear model for hoverfly abundance. In grazed treatments (a) hoverfly abundance increased, and in un-grazed treatments (b) showed little response to increasing tree/shrub species richness. Estimate = -0.766, SE = 0.307, *t* value = 2.497, *P* = 0.034, df = 9. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.7. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 14.

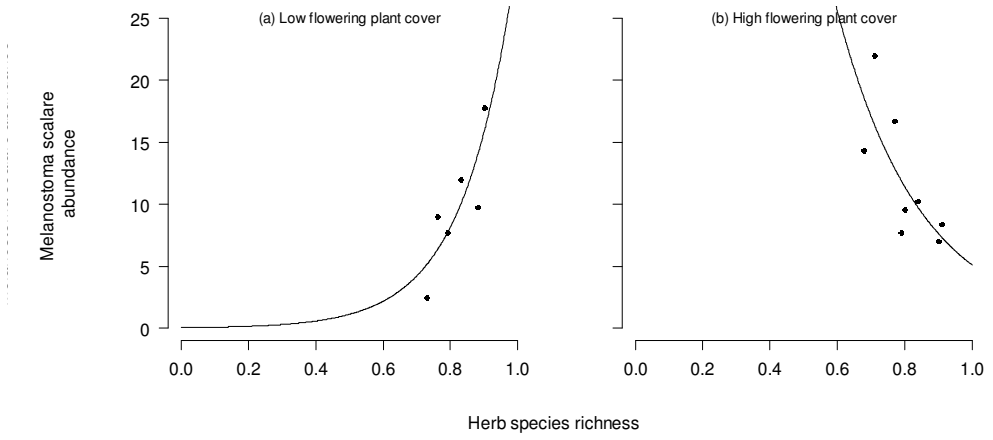


Figure 4. 15 The response of *Melanostoma scalare* abundance to the interaction between herb species richness and flowering plant cover. A significant effect of the interaction between herb species richness and flowering plant cover was detected in the generalised linear model for *Melanostoma scalare* abundance. Where flowering plant cover was low (a) there was an exponential increase, and where flowering plant cover was high (b) an exponential decline in abundance. Estimate = -0.581, SE = 0.096, *t* value = -6.072, *P* = < 0.001, df = 9. Low flowering plant cover ≤ 16 %, high flowering plant cover > 16 %, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.7. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 14.

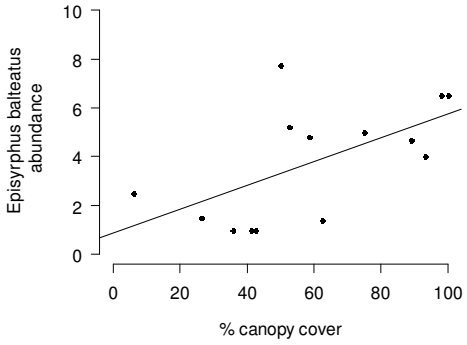


Figure 4. 16 The response of *Episyrphus balteautus* abundance to percentage canopy cover. A significant effect of percentage canopy cover was detected in the generalised linear model for *Episyrphus balteatus* abundance. Abundance increased in response to increasing canopy cover. Estimate = 0.013, SE = 0.006, *t* value = 2.328, *P* = 0.038, df = 12. Note that this figure does not take into account all the factors in the minimal adequate model shown in table 4.7, but is representative of the general underlying relationships. Line drawn is the regression of the relationship between the variables, n = 14.

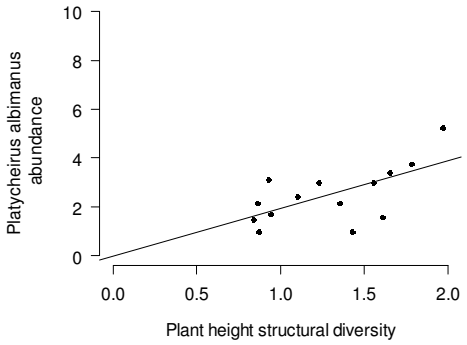


Figure 4. 17 The response of *Platycheirus albimanus* abundance to plant height structural diversity. A significant effect of plant height structural diversity was detected in the generalised linear model for *Platycheirus albimanus* abundance. Abundance increased in response to increasing plant height structural diversity. Estimate = 0.490, SE = 0.112, *t* value = 4.372, *P* = 0.003, df = 7. Note that this figure does not take into account all the factors in the minimal adequate model shown in table 4.7, but is representative of the general underlying relationships. Line drawn is the regression of the relationship between the variables, n = 14.

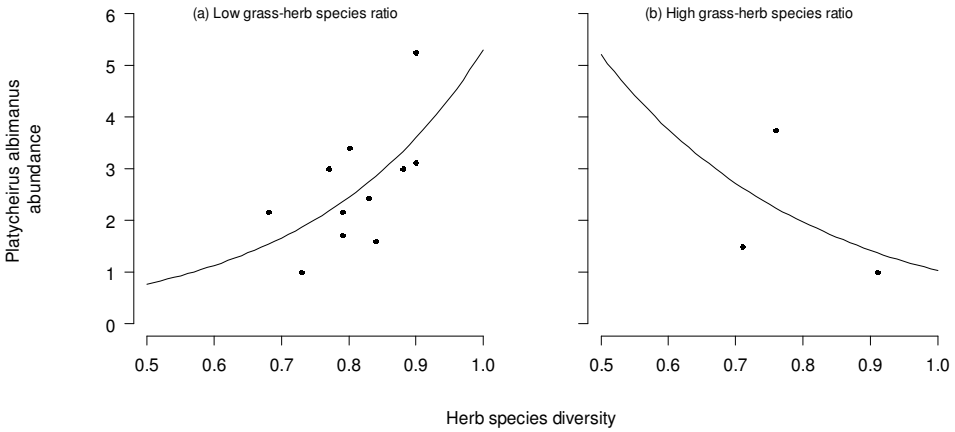


Figure 4. 18 The response of *Platycheirus albimanus* abundance to the interaction between the grass-herb species ratio and herb species diversity. A significant effect of the interaction between herb species diversity and the grass-herb species ratio was detected in the generalised linear model for *Platycheirus albimanus* abundance. Where the grass-herb species ratio was low (a) there was an increase, and where the ratio was high (b) there was a decline in abundance. Estimate = -57.608, SE = 7.967, *t* value = -7.231, *P* = < 0.001, df = 7. Low grass-herb species ratio ≤ 0.42, high grass-herb species ratio > 0.42, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.7. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 14.

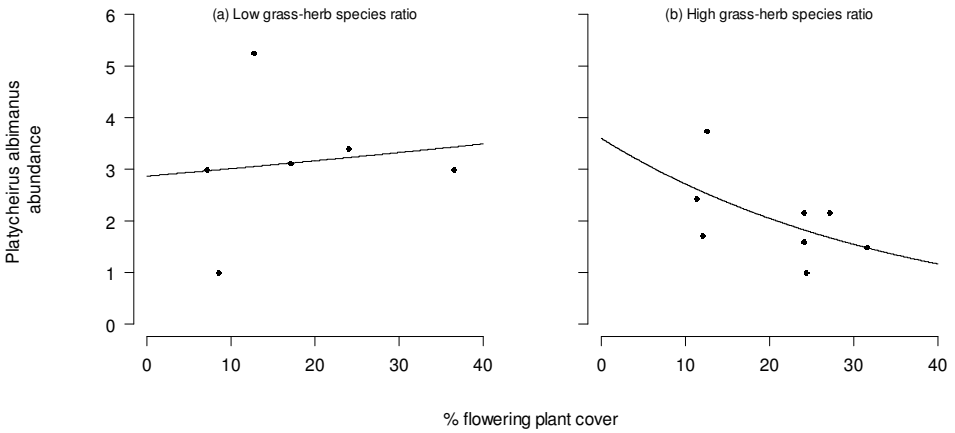


Figure 4. 19 The response of *Platycheirus albimanus* abundance to the interaction between the grass-herb species ratio and flowering plant cover. A significant effect of the interaction between flowering plant cover and the grass-herb species ratio was detected in the generalised linear model for *Platycheirus albimanus* abundance. Where the grass-herb species ratio was low, there was little change in abundance, and where the ratio was high there was a decline in response to increasing flowering plant cover. Low grass-herb species ratio ≤ 0.42, high grass-herb species ratio > 0.42, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.7. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 14.

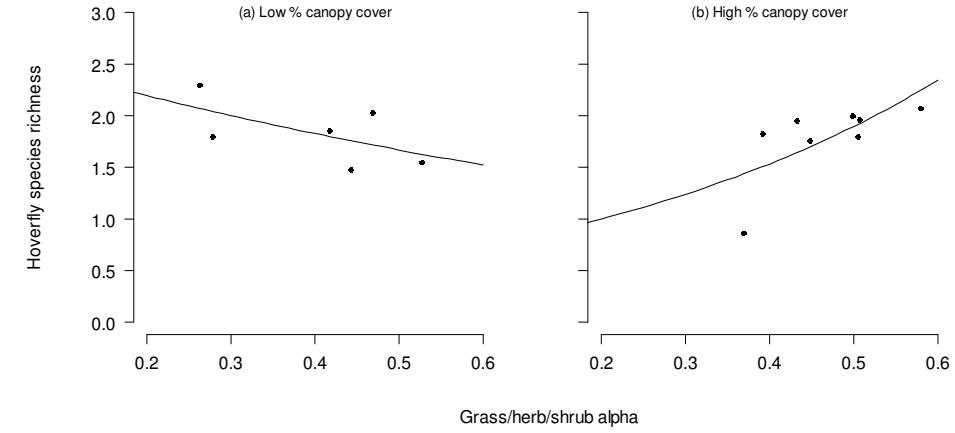


Figure 4. 20 The response of hoverfly species richness to the interaction between the diversity of the grass-herb-shrub structural gradient and canopy cover. A significant effect of the interaction between canopy cover and grass/herb/shrub alpha diversity was detected in the generalised linear model for hoverfly species richness. Where canopy cover was low there was a decline, and where canopy cover was high an increase in species richness in response to the grass/herb/shrub structural diversity. Estimate = 0.101, SE = 0.029, t value = 3.429, P = 0.006, df = 10. Low grass-herb species ratio ≤ 0.42, high grass-herb species ratio > 0.42, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.7. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 14.

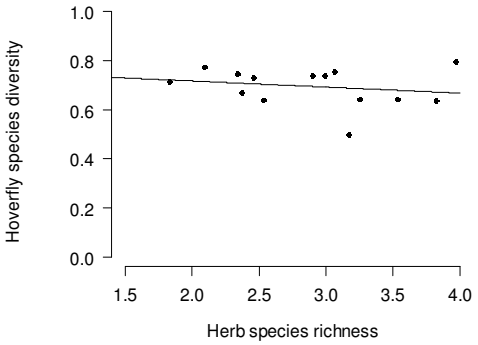


Figure 4. 21 The response of hoverfly species diversity to herb species richness. A significant effect of herb species richness was detected in the generalised linear model for hoverfly species diversity. Diversity declined in response to increasing herb species richness. Estimate = -0.114, SE = 0.023, *t* value = -5.064, *P* = 0.001, df = 9. Note that this figure does not take into account all the factors in the minimal adequate model shown in table 4.7, but is representative of the general underlying relationships. n = 14. Line drawn is the regression of the relationship between the variables, n = 14.

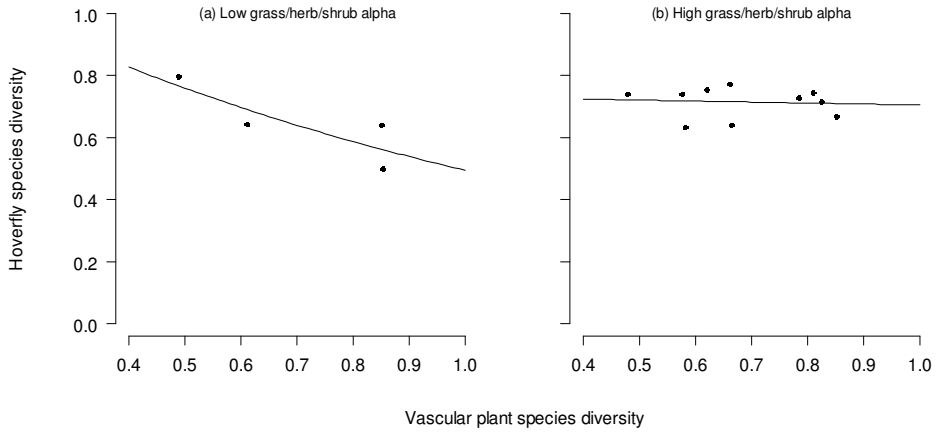


Figure 4. 22 The response of hoverfly species diversity to the interaction between the diversity of the grass-herb-shrub structural gradient and overall plant species diversity. A significant effect of the interaction between vascular plant species diversity (Simpson's D) and the grass/herb/shrub structure alpha diversity was delectated in the model for hoverfly species richness. Where grass/herb/shrub alpha was low, there was a decline, and where grass/herb/shrub/alpha was high, little response of diversity to increasing vascular plant species diversity. Estimate = 3.332, SE = 0.824, *t* value = 4.043, *P* = 0.003, df = 9. Low grass/herb/shrub alpha $\leq$ 0.42, high grass/herb/shrub alpha > 0.42, determined using a linear model to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 4.7. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasi-Poisson errors, therefore negative values are not predicted, n = 14.

Table 4. 10 Parasitoid abundance in the Letterewe oak woodland: effect sizes and their standard errors of significant explanatory variables. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Variable	Estimate	SE	T value	*P*	Res. Dev.	Df
Intercept	4.273	0.258	16.592	< 0.001 ***	1100.500	43
Plant species structural diversity	0.252	0.092	2.733	0.009 **		
May – June	-0.048	0.314	-0.153	0.879		
June – July	0.004	0.310	0.013	0.990		
July –August	0.588	0.273	2.151	0.037 *		
NVC W17a	0.045	0.282	0.159	0.875		
NVC W17c	-1.433	0.756	-1.894	0.065 .		
May - June : NVC W17a	0.171	0.397	0.430	0.669		
June - July : NVC W17a	0.295	0.388	0.761	0.451		
July - August : NVC W17a	-0.287	0.359	-0.798	0.429		
May - June : NVC W17c	2.262	0.824	2.744	0.009 **		
June - July : NVC W17c	2.277	0.820	2.775	0.008 **		
July - August : NVC W17c	1.530	0.813	1.882	0.067 .		

Notes: Minimal adequate model for parasitoid abundance as a function of plant species structural diversity and the interaction between sampling period and NVC community. Explanatory variables excluded during model simplification included plant species structural diversity : sampling round *(P = 0.814)*, sampling round : vascular plant species diversity *(P = 0.414)*, plant species structural diversity : vascular plant species diversity *(P = 0.253)*, vascular plant species diversity *(P = 0.659)*, sampling round : vegetation structural complexity *(P = 0.992)*, plant species structural diversity : vegetation structural complexity *(P = 0.351)*, vegetation structural complexity *(P = 0.759)*, sample period : grazing *(P = 0.607)*, plant species structural diversity : grazing *(P = 0.327)*, grazing *(P = 0.703)*, sample period : tree species richness *(P = 0.885)*, plant species structural diversity : tree species richness *(P = 0.525)*, sample period : tree species diversity *(P = 0.903)*, plant species structural diversity : tree species diversity *(P = 0.940)*, sample period : vascular plant species richness *(P = 0.432)*, plant species structural diversity: vascular plant species richness *(P = 0.231)*, sample period : grass/herb/shrub alpha *(P = 0.711)*, plant species structural diversity : grass/herb/shrub alpha *(P = 0.988)*, grass/herb/shrub alpha *(P = 0.576)*, plant species structural diversity : NVC community *(P = 0.186)*, sample period : bracken cover *(P = 0.669)*, NVC community : bracken cover *(P = 0.111)*, plant species structural diversity : bracken cover *(P = 0.768)*, bracken cover *(P = 0.884)*. See Chapter Two for a full explanation of each of the explanatory variables. Model of abundance data is a Generalized Linear Model with a quasi-Poisson error structure. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance. Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***.

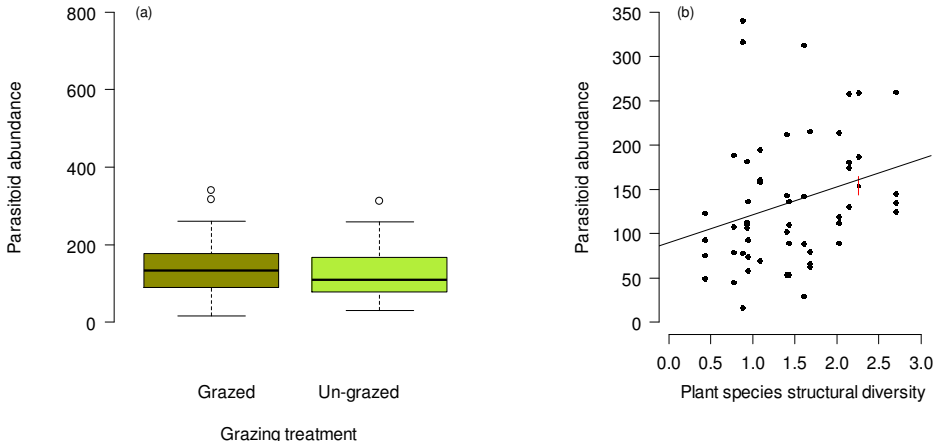


Figure 4. 23 The response of parasitoid abundance to (a) grazing, and (b) plant species structural diversity. No effect of grazing, and a significant effect of plant species structural diversity were detected in the generalised linear model for parasitoid abundance. Parasitoids were equally abundant in grazed and un-grazed treatments (a) Estimate (Grazed) = 4.267, (Un-grazed) = 4.212, SE = 0.143, t value = -0.383, *P* = 0.703, df = 50. and increased in abundance in response to increasing plant species structural diversity (b) Estimate = 0.252, SE = 0.092, t value = 2.733, *P* = 0.009. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002). Petals indicate where data points fall on exactly the same values of x and y. Note that this figure does not take into account all the factors in the minimal adequate model shown in table 4.8, but is representative of the general underlying relationships. Line drawn is the regression of the relationship between the variables, n = 56.

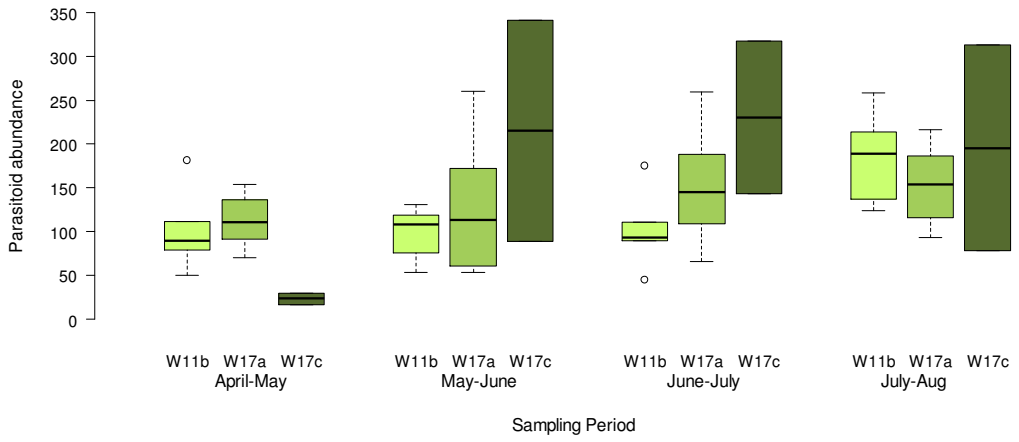


Figure 4. 24 The response of parasitoid abundance to sample period in woodland plant communities. A significant effect of the interaction between NVC community and sampling period was detected in the generalised linear model for parasitoid abundance. Parasitoid abundance ~ sample period (May-June) : NVC W17c (Estimate = 2.262, SE = 0.824, *t* value = 2.744, *P* = 0.009, df = 43). Parasitoid abundance ~ sample period (June - July) : NVC W17c (Estimate = 2.277, SE = 0.820, *t* value = 2.775, *P* = 0.008, df = 43). Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002). Note that these figures do not take into account all the factors in the full model shown in table 4.7, but are representative of the general underlying relationships. n = 56. NVC communities: W11b *Q. petraea - B. pubescens - Oxalis acetosela, Blechnum spicant* sub-community, W11c *Q. patraea – B. pubescens – Dicranum majus, Isothecium myosuroides – Diplophylum albicans* sub-community, W17a *Q. petraea – B. pubescens – Dicranum majus, Anthoxanthum odoratum – Agrostis capillaris* sub-community.

At the upper end of the range a negative relationship is cautiously predicted. In the interaction between the grass-herb species ratio and flowering plant cover, a positive correlation was observed where the ratio = 0, and a negative effect where the ratio > 0. Hoverfly species richness was predicted the interaction between the diversity of the grass-herb-shrub structural gradient and canopy cover (figure 4.20), with a negative effect observed were canopy cover was less than or equal to 50 percent, and a positive effect where canopy cover was greater than 50 percent. Hoverfly species diversity was negatively correlated with herb species richness (4.21), and in the interaction between total plant diversity and the diversity of the grass-herb-shrub structural gradient (figure 4.22), a negative correlation was observed at the lower end of the observed grass-herb-shrub-alpha, and little effect detected at the higher end of the range. The abundance of parasitoid wasps was unaffected by grazing, and displayed a clear increase in response to plant species structural diversity (figure 4.23b). In addition there was a significant effect of the interaction between NVC community and sampling period (figure 4.24). In all but the first period of sampling (April-May), the W17c sub-community had by far the greatest abundance of parasitoids. W17a ranked second in May-June and June July, third in July-August, and first in April-May. Interestingly the generally highest ranking W11c was markedly low in parasitoid abundance in April-May.

4.6 Discussion

Despite some significant effects on vegetation, experimental exclusion of deer had more subtle effects on invertebrate biodiversity in the Letterewe oak woodland. There was no evidence of any negative effects of grazing on invertebrate communities, and several important positive effects were observed, suggesting that in terms of the maintenance of invertebrate biodiversity, red deer grazing is preferable to grazing exclusion. Grazed treatments typically had higher abundance of invertebrates, and also higher richness and diversity, than experimentally fenced (un-grazed) plots, which was consistent with the findings of previous studies (Ings, 1999, Suominen, 2003, Gonzalez-Megias, 2004, Melis *et al.*, 2006, Olff and Ritchie, 1998, Rambo and Faeth, 1999). There were no instances of significantly lower invertebrate biodiversity in grazed plots compared to fenced plots.

Empirical evidence of determinants of carabid distributions provides plentiful explanations for this pattern. There is much evidence to suggest that carabid assemblages vary with the type and amount of vegetation cover and are characteristically specific to certain types (Taboada *et al.*, 2006). Many Carabid beetles have particular associations with damp and shade, and others more so with open dry conditions (Ings and Hartley, 1999) or

reduced vegetation cover (Suominen et al., 1999). Larger carabids preferentially feed on large plant bugs (Homoptera: Cicadellidae) (Lang et al., 1999) which are more abundant in structurally diverse vegetation (Cole, 2002) and it is likely that greater carabid abundance reflects the availability food sources. While structural complexity of the vegetation was in fact higher in un-grazed plots, due to removal of grazing pressure, the study by Cole relates to a grassland sward, and in this study the vegetation characteristic of grazed oak woodland is more similar to grassland than that that of fenced exclosures. Grazed plots may therefore be more abundant in food sources and preferable to carabids. Large carabid species also have long life cycles, often up to 2 years, and their slow growing larvae are less able to withstand drastic and sudden changes to habitat structure (Cole, 2002). Removal of grazing pressure causes dramatic changes in vegetation structure, and an associated cascade of microclimatic effects, which may be unfavourable to carabid larvae. Many carabids are visual hunters and are more abundant where there are patches of bare ground and vegetation structure is not prohibitive to foraging activities (Telfer M.G., 2000) which may partially explain the response in grazed treatments.

This study provides no evidence of reductions in invertebrate richness mediated by grazing causing the removal of host plant species or their replacement with unpalatable gramminoids and bracken (Stewart, 2001), however over a longer time scale this may start to occur. Greater floral diversity of the grazed sward may provide nectar resources throughout the flight period benefiting many adult invertebrates, and while this was not specifically tested, vascular plant species richness was higher in grazed treatments, and may hold the key to a floristic effect. The findings of this study are contradictory to those of one of only two studies to date that specifically consider the impact of red deer grazing in UK woodland. In native Scottish pine woodland Lepidoptera, Hymenoptera, Coleoptera, Areneae, Diptera and Plecoptera were all more abundant in grazing exclosures than grazed woodland, and grazed plots had lower heather and higher grass cover than exclosed or less heavily grazed plots (Baines *et al.*, 1994). These results from pine woodland are not directly comparable with the present study of Atlantic oak woodland, between which the vegetation and invertebrate community varies dramatically. There was also considerable variation in grazing pressure between grazed plots in their study, compared to that observed at Letterewe, which also compared East and West highland pinewoods, and examined only abundance, and not richness or diversity.

A number of vegetation characteristics had significant effects on invertebrates, generally concordant with classical studies. Vegetation structural complexity tended to

increase the abundance of invertebrates, independent of fencing treatment. This is in agreement with the theory put forward in the introduction of a direct increase in niche availability with greater structural complexity (Lawton and Schroder, 1977; Strong, 1984) and indirectly through alteration of microclimate effects, for example through shading, water uptake by trees, soil moisture regulation (Ings and Hartley, 1999) and the consequences for ground flora composition. The response of parasitoid abundance in particular, to vegetation structure, is in agreement with the findings of Fraser *et al.,* (2007) and Saaksjarvi *et al.,* (2006) who found a significant predictive capability of botanical composition. No general trend in invertebrate responses to plant species composition was apparent. There was significant variation in invertebrate biodiversity between the NVC vegetation communities, as might be expected. Increased botanical species richness may result in more heterogeneous habitat patches with increased prey diversity, abundance and niche availability that have classically been used to explain the former relationship, and is supported by the observed response of Coleoptera species richness. Conversely, increased botanical species richness may act to competitively reduce or exclude a particularly important food resource such as a plant that provides a substantial portion of the nectar requirements of adult hoverflies, or prey sources for larval hoverflies, and is suggested by the response of hoverfly species diversity.

Given the significant differences in some of the vegetation features between the treatments, it is surprising that many invertebrates were unaffected by grazing. In particular, the potential for grazing to impact the abundance of syrphids is great. Behavioural characteristics of *M. scalare*, *E. balteatus* and *P. albimanus* include flying low over vegetation, hovering beside bushes and in the shade of the canopy, and visiting a vast array of flowers. Larvae may occur predominantly in leaf litter or tussocks of grasses, and many are aphidophagous on a wide range of low-growing plants (Speight *et al.*, 1998). An obvious potential predictor of these species if the abundance of flower heads, shown to decline under red deer grazing (Virtanen *et al.*, 2002), and the diversity and percentage cover of flowering plants, herbs and the grass-herb species ratio (Kruess and Tscharntke, 2002). While flower head abundance was not specifically quantified here, floral resources eaten by deer include hawthorn *Crataegus monogyna,* blackthorn *Prunus spinosa,* elder *Sambucus nigra,* and species of the Umbelliferae and Compositae (Stewart, 2001), but in the Letterewe oak wood deer grazing pressure in the herb layer did not result in significant effects on flowering plant cover. This suggests that grazing pressure was insufficient to cause an effect. Many woodland Diptera suffer under conditions of increased solar penetration, as they require moist humid conditions for larval development, provided by a dense canopy, bushy shrub

layer, and lush herb layer, that are lost above a critical grazing threshold (Stewart, 2001). No evidence of this effect on the syrphids studied here was observed. Searching behaviour of parasitoids is affected by the architecture of prey host plants (Cloyd and Sadof, 2000) and adult parasitoids need sugar sources nectar honeydew floristic effects (Shaw, 2006) so it is surprising that given the difference in vegetation between treatments, no effect was observed.

4.6.1 Synthesis and applications

The key findings of this chapter provide strong support for the notion that grazing can be consistent with maintaining invertebrate diversity, and that of dependent trophic elements, and suggest that decreasing the number of deer using the woodland to levels that would allow vegetation succession similar to that inside exclosures would be detrimental to biodiversity in the short term. It seems likely that current deer usage of the habitat falls within the middle range of a gradient of grazing effect, concurrent with the intermediate disturbance hypothesis (Grime, 1973a), in which diversity is maximised under intermediate conditions of disturbance. These findings are in agreement with other studies that find maximum invertebrate community response under intermediate levels of grazing (Olff and Ritchie, 1998, Rambo and Faeth, 1999) and suggest that in respect of invertebrate biodiversity, the woodland is not overgrazed. There is consensus within the literature that biodiversity is often maximised under a gradient or mosaic of habitat elements (Lawton, 1998, Stewart, 2001, Sroka and Finch, 2006, Ings and Hartley, 1999). The mosaic may include different successional stages, or a variety of management prescriptions, for instance, in a mosaic of habitat types of different stages of regeneration in native Scottish forest (Ings, 1999) and under varied logging practises in ancient woodland remnants (Sroka and Finch, 2006). Habitat management prescriptions play an important role in determining vegetation structure, and the effect of grazing on vegetation and invertebrate communities has important consequences for conservation and management of other taxa. For example, forest grouse species such as capercaillie *Tetrao urogallus* are associated with bilberry, and their chicks feed on both vegetation and lepidopterous herbivores of bilberry (Baines *et al.*, 1994). While it was not possible here to investigate the entire set of invertebrate taxa, these results provide useful and consistent indications of grazing effects.

4.6.2 Limitations

The general limitations of the Letterewe oak woodland grazing exclosure experiment are applicable to both this and the following chapter, and as such are to be found in the discussion of Chapter Five. Due to the time constraints on this study it was not possible to

consider the implications of reducing or increasing deer numbers on invertebrates. An interesting concept to imagine is the complete exclusion of deer from the woodland and surrounding stalking beat for an extended period, of say 50 years. One might expect those areas of the woodland suitable for natural regeneration to proceed through succession, including a stage equivalent to that existing in the current exclosures, to climax woodland patches. These would probably consist of a much more species rich tree fauna than the closed canopy stand, and may include aspects of native Caledonian pine forest. Under the closed canopy the ground flora would likely remain little changed in comparison, except in areas where tree mortality and storm damage produced canopy gaps. The most dramatic change to the landscape might be the expansion of the wooded area to the extent of the natural tree line, as indicated by historical evidence, and currently limited by deer predation of seedlings, seed addition, and potentially vole predation (Milner *et al.*, 2002). What then would be the effect on biodiversity of this large scale successional progression and expansion of the woodland? Evidence from this study suggests that early successional stages similar to exclosures, would have reduced invertebrate biodiversity, but over the longer term at a landscape scale, biodiversity is likely to increase. Caledonian pine woodland supports a very different community to oak woodland, and more variety in the mixed deciduous element would again add a different assemblage. It is true that areas of valued heather moorland would be lost, but to the overall benefit of biodiversity. It seems desirable then to seek this progression, and that deer presence in the landscape contradicts this objective. In order to balance these aims with the opposing interests of deer stalking on their fulfilment, the continued use of exclosures, with un-exclosed areas in which deer can graze and shelter, offers a compromise by which both can be achieved. The complete exclusion of grazing in the short term would benefit only regeneration but not invertebrate diversity. There are other potential benefits of grazing exclosures; clearly regeneration is vital to the long term persistence of the woodland, and the different characteristics of the vegetation in exclosure plots may benefit animal populations other than those considered here, to a greater extent than grazed areas. The increased structural diversity inside exclosures creates exploitable niches with potential benefits to invertebrates not examined here, and the more extensive understory may provide cover, protection from predators, and nest sites for small mammals and birds. There was no evidence in this study of a positive effect of exclosures on invertebrate biodiversity, as might have been anticipated as a result of the increased overall habitat heterogeneity. Such an effect may however be observed in other taxa. The continued use of exclosures on a rotational basis effectively creates two distinct species reservoirs, from which inter-colonisation between

grazed and un-grazed patches can occur along a temporal management gradient. If the habitat is to be maintained for biodiversity, support an economically viable deer stalking enterprise, and continue to be part of the national heritage, the continuation of the current fencing and grazing policy offers the best solution. Grazing by wild ungulates should be viewed as integral to the fluid dynamics of vegetation regulation processes rather than a suppressing factor (Vera, 2000).

4.7 Conclusions

The effects of grazing by red deer in the Letterewe oak woodland, under the population density present during the study period, had no negative, and some beneficial effects on the invertebrate assemblages considered, when compared to un-grazed exclosure plots. These effects can be inferred upon other invertebrate groups, and are likely to percolate upwards through a trophic cascade. Grazing by red deer should be viewed as integral to the maintenance of invertebrate biodiversity in the Letterewe oak woodland.

Chapter 5

Invertebrate guild responses to grazing management in the Letterewe oak woodland.

Abstract

Presented here are the results of an experimental examination of invertebrate guild responses to grazing, which allowed investigation of competing groups of species that utilise similar ecological resources, out-with the constraint of taxonomic relatedness. Grazing exclosures resulted in some significant effects on the woodland vegetation, but were not associated with significant effects on any of the studied guilds. The main trends of grazing and vegetation variability effects on guild member abundance are consistent across all trophic levels. These results indicate that the management practise of using small scale grazing exclosures on a rotational basis in conjunction with grazed habitat patches is consistent with the maintenance of invertebrate guild structure and conservation in the Letterewe oak woodland, and that grazing has no detrimental effect on invertebrate biodiversity over the scale examined. This study also demonstrates the potentially important role of geotrupid dung beetles in providing ecosystem services in red deer grazed habitats, with particular reference to secondary seed dispersal, and highlights several areas that would benefit from further research.

5.1 Introduction

Habitat heterogeneity can produce a cascade of effects upwards through the trophic levels and this can affect functional guild responses to management. In contrast to taxonomic methods of examining community responses, typically by investigating species richness and diversity measures of particular groups of organisms, the guild concept takes a multi-taxon approach, grouping species with similar niche requirements, without regard for systematic

classification (Simberloff and Dayan, 1991). The terms "guild" and "functional group" are often used interchangeably, however the former refers more specifically to the competitive sharing of resources, while the latter relates to ecosystem services and to functions provided by the processing of resources carried out by the members of the group (Blondel, 2003). The advantage of using the guild concept when studying ecological communities is that guilds allow examination of groups of competing species, out with the constraint of taxonomic relationship. In comparative studies, it is typically impossible to study all species simultaneously, and guilds allow one to focus on groups with similar functional relationships and/or roles (Simberloff and Dayan, 1991). Species do not respond independently to disturbance, but as interacting groups of species (Voigt et al., 2007).

The guild concept is reviewed by Hawkins and Macmahon (1989) and has a long history in ecological research (Root, 1967, Grime, 1973b, Wilson, 1999, Hendrix *et al.*, 1988). It is a well established method used in the examination of communities, particularly invertebrates (Moran and Southwood, 1982, Grimbacher and Stork, 2007). Despite an arbitrary element to the assignation of species to guilds, it has proved an effective means of testing species assemblage responses to environmental change (Voigt et al., 2007).

Invertebrate guild structure varies between plant species within a genus, as demonstrated by a study of European oaks, which also found strong seasonal patterns in assemblage structure (Southwood et al., 2005). Conversely, in a study which examined the vertical stratification of arboreal arthropods in an Australian tropical rainforest, Grimbacher and Stork (2007) found little canopy-ground variation in feeding guild response, and suggest that much finer scale differences in resource partitioning, and the microclimatic gradient may be more significant predictors of assemblage structure than guild membership. On a large scale, functional guilds are a valuable component used in studies which seek to calibrate the use of data sets that measure the effects of anthropogenic disturbance in tropical forests (Basset et al., 2004).

Splitting seed-feeding insects into guilds allowed Fukumoto and Kajimura (2001) to identify seasonal trends in the guild use of acorns in two *Quercus* species, to find an effect of early season guild on the utilisation by another guild later in the development of a food resource, and to identify a potential advantage to one guild due to the absence of another in one oak species. A study which examined the consequences of cattle grazing and exclusion regimes in Argentina, found distinctive differences in trophic structure associated with heavy grazing (Cagnolo, 2002). Guild composition was similar between grazing excluded and extensively grazed montane grassland, but heavy grazing lead to an assemblage that was

impoverished in secondary consumers, and in which herbivores with chewing replaced those with sucking mouthparts. Various theories for the observed pattern have been proposed, based on the structural and species compositional aspects of the vegetation, mediated by the effects of grazing. The response of guild composition to spatial and plant community compositional variation is highlighted in a study that used a factorial design to investigate insect responses to habitat change in grassland (Crist et al., 2006). Habitat area was not a significant predictor of any of the guild responses examined, but vegetation characteristics significantly explained the variation in abundance of herbivorous insects, that were associated with legume and gramminoid cover, and in predators and parasitoids, associated with plant species richness and habitat edge effects. More recently, variation in guild response has been used to examine the efficacy of ecological compensation meadows on arthropod diversity in agri-ecosystems, and reports edge effects on guilds independent of taxonomic relatedness (Albrecht et al., 2010).

In this chapter life history trait responses of parasitoids and feeding guilds of syrphids and epigeal arthropods are used to investigate the impacts of red deer grazing management on the functional components of biodiversity in response to red deer grazing exclosure in the Letterewe oak woodland.

5.1.1 The coprophagous guild

Coprophages are animals that utilise dung as a food resource, and are easily manipulated in experiments designed to investigate the relationships between species and guilds, with ecosystem processes. This allows scientists to make predictions concerning the effect of habitat management and community structure on ecosystem functions and services. Changes in assemblage characteristics through human impacts such as habitat disturbance, management, or natural processes such as grazing, may have important consequences for the ecosystem services provided by biodiversity (Loreau et al., 2001). Interspecific variation in resources processing, intraspecific interactions, and impacts on the physical environment are potential mechanisms by which species richness may affect functional processes (Larsen et al., 2005). Herbivores such as deer are able to indirectly influence processes such as nutrient cycling and decomposition through their quantitative and qualitative control of resource inputs such as dung (Harrison and Bardgett, 2003a). Deer produce large quantities of dung which attracts a diverse range of coprophagous invertebrates, the most conspicuous of which are dung beetles in the genera Geoptrupidae and Scarabaeidae (Stewart, 2001). In the Letterewe oak woodland extensive pitfall trapping revealed that while diverse, the

coprophagous Coleoptera fauna was most conspicuously represented by one species *Geotrupes stercorosus*. Dung feeding beetles are highly sensitive to changes in dung resources (Nichols et al., 2008) and anthropogenic disturbance (Scheffler, 2005). In the UK, two nationally scarce species are specifically associated with deer dung, certain Staphylinidae prey on invertebrates found in dung, and a distinct dipteran fauna also utilise this resource. In many woodlands, deer are the primary or sole source of dung, and the widespread use of avermectins to control intestinal parasites of grazing livestock mean that deer dung may provide refugia for coprophagous invertebrates on which these chemicals have a detrimental impact (Stewart, 2001). Invertebrates found in association with dung provide an important component of the diet of predatory vertebrates at crucial times of the year. Dor beetles (Geotrupid and Typhoues spp.) accounted for more than 50% of prey items in the winter diet of tawny owls *Strix aluco* due to a temporal scarcity of small rodents in the New Forest, Hampshire, while Aphodius spp. have been found to comprise an important alternative food source for the threatened greater horseshoe bat *Rhinolophus ferrumequinum* between July and October, a period when females are under severe physiological stress as lactation progresses, (Stewart, 2001). Dor beetles are also utilised by this species during periods of emergence from winter hibernation, while several other species of bats are also thought to make use of insects associated with dung.

5.1.1.1 The ecology of dung removal

Through manipulation of faeces during the feeding process, removal of dung can provide valuable ecosystem services such as biological pest control, soil fertilization, bioturbation, plant growth enhancement, secondary seed dispersal and parasite control, as well as playing a more limited role in pollination and trophic regulation (Shepherd and Chapman, 1998; Andresen, 2003; Nichols et al., 2008). The excreta voided by vertebrates contains a substantial proportion of the nutrients that were consumed, and the redistribution of these throughout the plant growth cycle is an important limiting factor on primary production. The removal of waste below the soil surface by dung beetles allows micro-organismal and chemical breakdown of the nutrient rich material, making resources available to plants (Nichols et al., 2008). Tunnelling species of dung beetle displace and mix sediment particles contributing to bioturbation that can influence soil-dwelling organisms and plant productivity by increasing soil aeration and water porosity (Nichols et al., 2008). There is much evidence reporting significant yield increases as a result of dung beetle facilitated nutrient mobilisation of dung in agricultural systems, although there is a lack of evidence in natural, particularly

tropical forest conditions (Nichols et al., 2008). Other influences include parasite suppression, for example by reducing the abundance of helminth eggs that pass through the gut of the beetle, parasite dispersal through the action of transporting dung-borne pathogens either internally or externally, and control of flies through direct competition for dung resources, mechanical destruction of dipterous eggs, and predation of flies by mites phoretic on dung beetles (Nichols et al., 2008). Lastly, some dung beetles are unique in having roles in trophic regulation, through predation of leaf cutter ant queens of the genus *Atta*, a principle herbivore in the Neotropics, and although rare, some species have obligate pollinator roles for decay-scented flowers (Nichols et al., 2008).

5.2 Aims

The hypothesis that the ecosystem modifying processes brought about by deer grazing may alter habitat conditions such as vegetation architecture and species diversity, which in turn affect the availability of resources to invertebrates, such that different invertebrate guilds will respond to deer exclusion in distinctive and possibly contrasting ways, was tested. The aim was to examine these effects on functional traits of the hoverfly, epigeal arthropod, and parasitoid assemblage of the Letterewe oak woodland, which will provide a useful tool with which to examine the impact of grazing management on biodiversity. The aims of this chapter are:

- To assess the role of fencing to exclude grazing as a red deer management practise in impacting functional responses of invertebrate diversity in the Letterewe oak woodland.
- To determine the factors affecting the variation in guild responses in the Letterewe oak woodland.
- To quantify the contribution of geotrupid dung beetles, and the influence of grazing exclosures on the removal of red deer dung pellet groups, and discuss the potential consequences for ecosystem functional processes.
- To make recommendations for planning and management of the Letterewe oak woodland to maintain guild composition.

The hypotheses that guild structure does not vary between grazed and un-grazed woodland plots, and shows no association with habitat variables, and that there is no effect of geotrupid beetles, or grazing treatment, on removal rates of experimental dung pellet groups were tested. By identifying the primary components that determine guild composition and function

in the Letterewe oak woodland, it will be possible more effectively to assess the consequences of management practises and grazing policy for biodiversity in red deer habitats.

5.3 Methods

Epigeal invertebrates, syrphids and parasitoids were sampled using both pitfall traps and malaise traps, in grazed and un-grazed exclosure plots ranging in age from one to fifteen years, in the Letterewe oak woodland in 2007 and 2008. Details of the study site, general sampling methods and habitat survey methods can be found in Chapter Two.

5.3.1 Invertebrate guilds used in this study

The assignation of species to guilds is frequently carried out using quantitative methods and multivariate statistics such as nearest neighbour, clustering, principle components analysis, canonical correlation, or Monte Carlo techniques. While explicit, these methods are not unambiguous in their determination of guilds, as the investigator specifies arbitrary levels of the factors used for clustering (Simberloff and Dayan, 1991). Here it was preferred to partition species into broad yet functionally specific and unambiguous feeding guilds, based on robust data sourced from the literature, and to carry out analysis on the abundances of guild member species. Hoverflies were split into feeding guilds based on larval food type information taken from the Syrph the Net database (Speight *et al.*, 1998). Epigeal arthropods were assigned to guilds based on adult feeding preferences using data from the literature (Ribera *et al.*, 1999). The definition of parasitoid guilds is determined by three parameters – host stage attacked, host stage killed, and type of parasitism (either internal or external larval development) (Mills, 1994). Based on these parameters 12 parasitoid guilds are recognised at the genus level. Here parasitoids were identified to sub-family level, and consequently 6 guilds were distinguishable, based on life history traits (Gauld and Bolton, 1988, Shaw and Huddleston., 1991, Saaksjarvi *et al.*, 2006). The Phrudinae and Tersilochinae were aggregated on the basis of shared traits (Quicke et al., 2009). Details of the guilds examined and the identity of guild members can be found in tables 5.1 to 5.3.

5.3.2 Manipulation of coprophagy

Beetles of the genus Geotrupidae were by far the most abundant coprophagous species captured in pitfall traps at the study site and can easily be separated from other dung feeders by their size. Standard pitfall trapping (Woodcock, 2004) at the site using pitfall traps baited with a mixture of homogenised red deer and horse dung set from July until September 2008

did not result in the addition of any coprophagous beetle species to the list of 33 species previously known from the site (Milner *et al.*, 2002). The experiment used an exclosure designed to restrict access to experimental dung pellet groups based on the size of beetles, to investigate a two factor interaction on dung removal with aim of quantifying the relative contribution of Geotrupid dung beetles, and the impact of habitat management with grazing exclosures, on rates of dung removal. Galvanised wire mesh cages with a mesh size of 5 mm were used to exclude Geotrupid beetles from experimental deer pellet groups. Control wire mesh cages with a mesh size of 15 mm were used, which allowed all sizes of dung feeding Coleoptera to pass through the mesh. The cages were tested in the field with live caught Geotrupids to ensure they could not pass through the 5 mm mesh. A literature search of coprophagous beetles known from the study site (Milner *et al.*, 2002), data from the Biological Records Centre, and personal identification of dung beetles caught in 10 standard pitfall traps baited with red deer dung pellets in 2008, were used to determine the maximum size of all other dung feeding Coleoptera species, such that all but the Geotrupids were considered able to pass through the 5 mm mesh.

Red deer dung pellets were collected from one field on the estate, and mixed to reduce the potential variation between experimental pellet groups. Pellets were collected on one day, from a field used by a limited number of deer, so that individual variation in pellet characteristics was controlled for as far as possible. It was not possible to collect pellets from one individual. Pellets were frozen for a minimal of 96 h to kill any coprophages or predators already present, and moisture removed by drying for 48 h. A mean dry pellet group weight of approximately 200 g was determined from dung collected in the field (n = 15 pellet groups) and used to quantify the size of the experimental pellet groups, so that experimental pellet groups were equivalent in size to those occurring naturally. 28 pellet group replicates were placed in cages the field, in each of the exclosed and un-exclosed sample plots, one small and one large mesh cage in each plot in a nested split plot design. After the first substantial rainfall pellet groups were considered to have absorbed moisture consistent with pre-drying saturation levels and cages were then covered to prevent breakdown of pellets by precipitation. Pellet groups were left in situ from May until September when they were collected, re-dried and weighed. The effect of evaporation on pellet groups over this period was considered negligible therefore estimates of weight loss due to water loss were considered unnecessary. The abundance of *Geotrupid* spp. was determined from data collected in the study detailed in Chapter Four.

Table 5. 1 The assignation of orders, sub-families and species of epigeal woodland invertebrates captured by pitfall trapping to guilds.

Predatory	Herbivorous	Coprophagous	Necrophagous	Detrivorous
Eutrombidium spp.	Mollusca	*Aphodius rufipes*	*Hister striola*	Diplopoda
Areneae	*Agriotes obscurus*	*Geotrupes stercorarius*	*Nicrophorus humator*	Isopoda
Staphylinidae	*Amara communis*	*Geotrupes stercorosus*	*Nicrophorus investigator*	
Chilopoda	*Amara lunicollis*	*Serica brunnea*	*Nicrophorus vespilloides*	
Abax parallelepipedus	*Athous haemorrhoidalis*		*Oiceoptoma thoracica*	
Agabus guttatus	*Barynotus squamosus*		*Silpha atrata*	
Calathus micropterus	*Burrhus pilula*		*Silpha obscura*	
Calathus rotundicollis	*Cantharis nigricans*			
Carabus clathratus	*Cantharis paludosa*			
Carabus glabratus	*Chrysolina staphylea*			
Carabus granulatus	*Ctenicera cuprea*			
Carabus nemoralis	*Dalopius marginatus*			
Carabus problematicus	*Dascillus cervinus*			
Carabus violaceous	*Harpalus latus*			
Cychrus caraboides	*Hypnoides riparius*			
Dromius quadrimaculatus	*Melanotus rufipes agg*			
Leistus fulvibarbis	*Othius punctatulus*			
Leistus rufecens	*Otiorhynchus scaber*			
Loricera pilicornis	*Otiorhynchus singularis*			
Nebria brevocolis	*Otiorhynchus sulcatus*			
Poecilus cupreus	*Prosternon holosericeus*			
Pterostichus diligens	*Selatosomus impressus*			
Pterostichus madidus	*Strophosoma melanogrammum*			
Pterostichus melanarius				
Pterostichus niger				
Pterostichus nigrita				
Pterostichus strenuus				

Table 5. 2 The assignation of species of woodland syrphids captured using malaise traps to guilds.

Predatory	Microphagous	Herbivorous	Saproxylic
Baccha elongata	*Chalcosyrphus nemorum*	*Cheilosia longula*	*Chalcosyrphus nemorum*
Dasysyrphus albostriatus	*Eristalis pertinax*	*Cheilosia scutellata*	*Ferdinandea cuprea*
Dasysyrphus hilaris	*Ferdinandea cuprea*	*Melanostoma mellinum*	*Myathropa florea*
Dasysyrphus pinastri	*Myathropa florea*	*Melanostoma scalare*	*Sphegina clunipes*
Dasysyrphus tricinctus	*Rhingia campestris*		*Xylota jakutorum*
Dasysyrphus venustus	*Sericomyia lappona*		*Xylota segnis*
Didea fasciata	*Sericomyia silentis*		
Epistrophe grossulariae	*Sphegina clunipes*		
Episyrphus balteatus	*Xylota jakutorum*		
Eupeodes corollae	*Xylota segnis*		
Eupeodes lundbecki			
Eupeodes luniger			
Melangyna lasiophthalma			
Melanostoma mellinum			
Melanostoma scalare			
Meliscaeva auricollis			
Meliscaeva cinctella			
Parasyrphus punctulatus			
Platycheirus albimanus			
Platycheirus nielseni			
Platycheirus peltatus			
Platycheirus scutatus			
Syrphus ribesii			
Syrphus torvus			
Syrphus vitripennis			
Xanthandrus comtus			

Table 5. 3 The assignation of woodland parasitoid sub-families captured using malaise traps to guilds.

Idiobiont	Koinobiont	Ectoparasitic	Endoparasitic	Symphytophagous	Coleopteraphagous
Braconinae	*Adelognathinae*	*Adelognathinae*	*Agathidinae*	*Adelognathinae*	*Blacinae*
Cryptinae	*Agathidinae*	*Braconinae*	*Anomaloninae*	*Ctenopelmatinae*	*Ephialtini*
Ephialtini	*Alysiinae*	*Cryptinae*	*Aphidinae*	*Tryphoninae*	*Helconinae*
Euphorinae	*Anomaloninae*	*Ephialtini*	*Banchinae*		*Tersilochinae*
Exothecinae	*Aphidinae*	*Exothecinae*	*Blacinae*		*Xoridinae*
Hormiinae	*Banchinae*	*Tryphoninae: Netelia*	*Campopleginae*		
Pimplini	*Blacinae*	*Hormiinae*	*Charmontinae*		
Rhysipolinae	*Brach.(open)*	*other.Tryphoninae*	*Collyrinae*		
Xoridinae	*Campopleginae*	*Rhysipolinae*	*Ctenopelmatinae*		
	Charmontinae	*Xoridinae*	*Cylloceriinae*		
	Collyrinae		*Diosp.(closed)*		
	Ctenopelmatinae		*Diplazontinae*		
	Cylloceriinae		*Eucerotinae*		
	Diosp.(closed)		*Euphorinae*		
	Diplazontinae		*Ophioninae: Enicospilus*		
	Eucerotinae		*Ophioninae: Ophion*		
	Ophioninae: Enicospilus		*Helconinae*		
	Tryphoninae: Netelia		*Homolobinae*		
	Ophioninae: Ophion		*Ichneumoninae*		
	Helconinae		*Macroceentinae*		
	Macroceentinae		*Mesochorinae*		
	Mesochorinae		*Meteorinae*		
	Meteorinae		*Metopiinae*		
	Metopiinae		*Microgastrinae*		
	Microgastrinae		*Opiinae*		
	Opiinae		*Orthocentrinae*		
	Orthocentrinae		*Pimplini*		
	other.Tryphoninae		*Rogadinae*		
	Rogadinae		*Tersilochinae*		
	Tersilochinae				

5.3.3 Statistical analysis

Statistical analyses were performed using the software R 2.10.1 for Windows (R Development Core Team, 2010) following established techniques (Sokal and Rohlf, 1995, Crawley, 2007). To test the hypotheses that guild characteristics showed no response to grazing treatment or other habitat variation, Generalised Linear Models (GLM's) were used. Analysis of abundance data were performed using GLM's with a Poisson error structure, appropriate for count data, or quasipoisson where there was over dispersion in the response, as was typical. Initially all explanatory variables and quadratic terms for continuous variables were fitted individually to test for significance, and graphical inspection used to look for curvature in the response. Tree models were used to obtain a preliminary ranking of the

importance of the explanatory variables in order to distinguish those that best explained the variation in the data, and these used for initial parameterisation of GLM's. A top down model of all explanatory terms was then fitted to the data including interaction terms, limited to two-way terms, as far as replication in the data would allow. The least significant, highest order interactions were removed sequentially until all remaining terms were significant at $P < 0.05$ to produce the minimal adequate model (MAM). All MAM's were checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity, and the ordered residuals against the normal scores to look for evidence of non-normality of errors. Where heteroscedasticity occurred the response variable was transformed and goodness of fit reassessed. Models were compared using ANOVA to justify retaining or excluding variables, and Akaike's information criterion (AIC) used to compare model fit for models with a normal or Poisson error structure. Where the ANOVA indicated no significant difference between the models ($P > 0.05$) the model with the highest degrees of freedom was retained. Where a significant difference occurred the model with the lowest residual deviance was retained. To plot graphical representations of significant interactions, linear models were used to determine the threshold value above and below which splitting the variable the difference between models was most significant. Lines fitted are either regression lines, or fitted using the predict function in R to plot the model from the data. To test the hypotheses that dung removal rates showed no difference in response to Geotrupid spp. exclusion, grazing treatment, and other habitat variables, a Generalised Linear Model was used. As the error structure was not improved with transformation of the response, analysis of the dung removal data were performed using GLM with a normal error structure. A tree model was used to assess the explanatory variables in order to distinguish those that best explained the variation in the data, and these used for initial parameterisation of the GLM. A top down model of all explanatory terms was then fit to the data including interaction terms, and inclusion of interactions limited to two-way terms, as far as replication in the data would allow. The least significant, highest order interactions were removed sequentially until all remaining terms were significant at $P < 0.05$ to produce the minimal adequate model (MAM). The MAM was checked for goodness of fit by plotting the residuals against the fitted values to look for evidence of heteroscedasticity, and the ordered residuals against the normal scores to look for evidence of non-normality of errors. Models were compared using ANOVA to justify retaining or excluding variables, and Akaike's information criterion (AIC) used to compare model fit. Where the ANOVA indicated no significant difference between the models ($P > 0.05$) the model with the highest degrees of

freedom was retained. Where a significant difference occurred the model with the lowest residual deviance was retained.

5.4 Results

5.3.4 Grazing effects

Despite the differences in vegetation between the fenced and un-fenced treatments, there were no significant differences in the abundance of members of any of the 16 guilds whose response was examined, between grazed and un-grazed plots fenced to exclude red deer (figure 5.1, 5.6 and 5.10).

5.3.5 Epigeal invertebrates

Predatory epigeal invertebrates responded negatively to bryophyte cover (figure 5.2a), and positively to canopy cover (figure 5.2b). Herbivorous epigeal invertebrates were more abundant in 2008 than in 2007 (figure 5.3a), and responded to the interaction between leaf litter and bryophyte cover (figure 5.4). Where bryophyte cover was low, herbivores declined in response to leaf litter, and where bryophyte cover was high, epigeal herbivores increased in abundance in response to leaf letter cover. Coprophagous epigeal invertebrates, a guild which consisted almost exclusively of one Coleoptera species *Geotrupes stercorosus,* declined linearly in abundance in response to both bryophyte cover (figure 5.5a), and plant species structural diversity (5.5b), and increased linearly in response to grass/herb/shrub alpha structural diversity (5.5c). Necrophagous epigeal invertebrates were significantly more abundant in 2007 than in 2008 (figure 5.3b), and were not predicted by any other variable.

5.3.6 Syrphidae

Syrphids whose larvae feed on microorganisms responded to three two-way interactions. Firstly, to the interaction between tree-shrub species diversity and grass-herb species ratio (figure 5.7a); Where the grass-herb ration was low (≤ 0.14) there was an exponential increase in their abundance in response to tree-shrub species richness, and a gentle decline where the ratio was > 0.14. Secondly, to the interaction between tree-shrub species richness and grass/herb/shrub alpha structural diversity (figure 5.7b); Where the alpha structural diversity was ≤ 4, there was a gentle increase, and where alpha structural diversity was > 4 this became a much steeper exponential increase. Lastly, to the interaction between herb species richness and grass/herb/shrub alpha structural diversity (figure 5.7c); Below or equal to an alpha value of 4 the relationship was strongly positively exponential, and above 4 a more gentle but substantial decline. The abundance of adult syrphids with herbivorous larvae was predicted

by a single interaction, between vascular plant species richness, and plant species structural diversity (figure 5.8). Where the vegetation structure index was low (≤ 1.1) abundance declined exponentially in response to plant species richness, and increased linearly where the index was greater than 1.1. The abundance of adults whose larvae are saproxilic showed a strong positive relationship with plant height structural diversity (figure 5.9a), and those with predatory larvae similarly so in response to grass/herb/shrub alpha structural diversity (figure 5.9b).

5.3.7 Parasitica

Idiobiont parasitoid abundance responded to two interactions involving the NVC vegetation community. Firstly with plant species structural diversity (figure 5.11), there were strong positive relationships in both the W11b *Q. petraea - B. pubescens - Oxalis acetosela, Blechnum spicant* sub-community and the W17a *Q. patraea – B. pubescens – Dicranum majus, Isothecium myosuroides – Diplophylum albicans* sub-community, while in contrast the response in the W17c *Q. petraea – B. pubescens – Dicranum majus, Anthoxanthum odoratum – Agrostis capillaris* sub-community was a strong exponential decline. The second interaction that predicted idiobiont parasitoid abundance involved sampling period (figure 5.12). The general pattern was one of increased abundance from W11b, through W17a, being greatest in W17c, and of June-July and July-August the most abundant periods. The was a marked contrast however in the earliest sampling period, where the pattern of abundance reversed, being greatest in W11b, through W17a, and lowest in W17c. Koinobiont parasitoid abundance increased in response to two vegetation structural complexity variables, gently linearly with grass/herb/shrub alpha structural diversity (figure 5.13a), and more markedly so with plant species structural diversity (figure 5.13b). Two interactions with sampling period also predicted koinobiont abundance. The relationship between sampling period and NVC vegetation community (figure 5.14) was almost identical to that observed for idiobionts, differing only in overall abundance, and the order of community during July-August. Additionally, the response of koinobionts was negatively linear in April-May, May-June and June-July, while in July-August it reversed almost imperceptivity, however significantly, to positively linear. Both ecto- (figure 5.16a) and endo- (figure 5.16b) parasitoid abundance was positively linear with plant species structural diversity, and both displayed the same general pattern as idiobionts and koinobionts to the interaction between NVC vegetation community and sampling period (figure 5.17). The response of endoparasitoids to the interaction between tree species richness and sampling period (figure 5.15) was also identical in pattern

to that displayed by koinobionts. Symphytophageous parasitoids increased in abundance as sampling progressed through April to July (figure 5.20), at which point the relationship became asymptotic through until August. One interaction had a significant effect on their abundance (figure 5.21). Where plant height diversity was low, there was an exponential increase in response to vascular plant species diversity, and when plant height diversity was high this became less strongly positively linear. Finally, coleopterophagous parasitoid abundance was predicted by two interactions with sampling period. Firstly, with grass/herb/shrub alpha structural diversity (figure 5.22) the relationship was positively exponential in April-May, and positively linear in June-July, while conversely in May-June and July-August it is negatively linear. In response to vascular plant species diversity, abundance decreases exponentially in April-May, and slightly negatively linearly in June-July, which contrasts with slight increase in May-June and July-August (figure 5.23).

Table 5. 4 Abundance, standard errors and sample sizes of guild members trapped in grazed and un-grazed woodland exclosure treatments plots in 2008. Mean: arithmetic mean, SE: Standard error, n: sample size.

		Grazed				Un-grazed			
Zone/taxa	**Guild**	**Mean**		**SE**	**n**	**Mean**		**SE**	**n**
Epigeal	Predators	1515.77	±	257.01	13	903.27	±	182.042	11
	Herbivores	51.23	±	14.9	13	37.82	±	11.58	11
	Coprophages	186.31	±	42.6	13	85.45	±	28.951	11
	Necrophages	54.77	±	10.88	13	52.91	±	12.977	11
	Detritivores	162.15	±	44.76	13	249.09	±	105.406	11
Syrphidae	Microphagous	1.09	±	0.26	8	1.75	±	0.56	6
	Herbivores	9.41	±	1.66	8	10.35	±	1.618	6
	Saproxylic	0.75	±	0.19	8	1.44	±	0.503	6
	Predators	19.66	±	2.92	8	19.44	±	3.301	6
Parasitoids	Idiobiont	28.91	±	2.62	32	24.83	±	2.647	24
	Koinobiont	91.03	±	11.16	32	85.33	±	11.255	24
	Ectoparasitic	33.81	±	11.46	32	29.75	±	11.751	24
	Endoparasitic	108.34	±	3.32	32	96.54	±	3.199	24
	Symphytophgous	25.31	±	5.34	32	20.67	±	3.804	24
	Coleoptrophagous	4	±	0.52	32	3.79	±	0.678	24

Table 5. 5 Effect sizes and their standard errors of habitat variables on epigeal invertebrate feeding guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Guild	Estimate	SE	*t* value	*P*		Res. Dev.	Df
Predators							
Intercept	6.468	0.332	19.463	< 0.001	***	7481.5	21
Bryophyte cover	-0.014	0.006	-2.511	0.020	*		
Canopy cover	0.017	0.005	3.508	0.002	**		
Herbivores							
Intercept	-3595	730.3	-4.922	< 0.001	***	250.02	19
Bryophyte cover	-0.043	0.011	-3.849	0.001	**		
Year	1.793	0.364	4.930	< 0.001	***		
Leaf litter cover	-0.083	0.032	-2.590	0.018	*		
Bryophyte cover : leaf litter cover	0.002	0.001	2.620	0.017	*		
Coprophages							
Intercept	4.478	0.750	5.968	< 0.001	***	1632.1	20
Bryophyte cover	-0.034	0.011	-3.192	0.005	**		
Plant species structural diversity	-1.204	0.402	-2.994	0.007	**		
Grass/herb/shrub alpha	7.507	2.388	3.144	0.005	**		
Necrophages							
Intercept	1826.666	480.667	3.800	0.001	***	390.4	22
Year	-0.908	0.240	-3.792	0.001	**		
Detritivores	No significant predictors.						

Notes: Minimal adequate models for (a) predatory epigeal invertebrate abundance as a function of bryophyte cover and canopy cover. Explanatory variables excluded during model simplification included bryophyte cover : canopy cover (P = 0.541), bryophyte cover : tree species richness (P = 0.166), canopy cover : tree species richness (P = 0.126), tree species richness (P = 0.636), bryophyte cover : grazing (P = 0.543), canopy cover : grazing (P = 0.164), grazing (P = 0.117), bryophyte cover : year (P = 0.565), canopy cover : year (P = 0.138), year (P = 0.473), bryophyte cover : tree species diversity (P = 0.937), canopy cover : tree species diversity (P = 0.052), tree species diversity (P = 0.698), canopy cover : vascular plant species richness (P = 0.383), bryophyte cover : vascular plant species richness (P = 0.302), vascular plant species richness (P = 0.766), canopy cover : vascular plant species diversity (P = 0.950), bryophyte cover : vascular plant species diversity (P = 0.125), vascular plant species diversity (P = 0.432), canopy cover : vegetation height structural diversity (P = 0.252), bryophyte cover : plant species structural diversity (P = 0.637), canopy cover : plant species structural diversity (P = 0.241), plant species structural diversity (P = 0.069), bryophyte cover : grass/herb/shrub alpha (P = 0.396), canopy cover : grass/herb/shrub alpha (P = 0.167), grass/herb/shrub alpha (P = 0.484), canopy cover : NVC community (P = 0.212), bryophyte cover : NVC community (P = 0.310), NVC community (P = 0.152), canopy cover : bracken cover (P = 0.833), bryophyte cover : bracken cover (P = 0.386), bracken cover (P = 0.166), bryophyte cover : leaf litter cover (P = 0.063), canopy cover : leaf litter cover (P = 0.331), leaf litter cover (P = 0.156). (b) herbivorous epigeal invertebrate abundance as a function of year, and bryophyte cover: leaf litter cover. (c) coprophagous epigeal invertebrate abundance as a function of bryophyte cover, plant species structural diversity and grass/herb/shrub alpha. (d) necrophagous epigeal invertebrate abundance as a function of year. None of the explanatory variables used in the model significantly predicted the abundance of detrivorous epigeal invertebrates. Model simplification for all models follows the same protocol as (a). See Chapter Two for a full explanation of each of the explanatory variables. Models of abundance data are Generalized Linear Models with a quasipoisson error structure.

Table 5. 6 Non-significant grazing exclosure treatment effects on epigeal invertebrate feeding guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Epigeal guild	Estimate	SE	*t* value	*P*		Res. Dev.	df
Predators	-0.355	0.217	-1.640	0.117	ns	6636.6	20
Herbivores	3.936	0.270	14.591	0.000	ns	1083.3	22
Coprophages	-0.544	0.359	-1.514	0.146	ns	1444.3	19
Necrophages	-0.092	0.242	-0.380	0.708	ns	379.96	20
Detritivores	0.335	0.506	0.662	0.516	ns	5021	19

Notes: Note: Asterisks indicate the level of significance: *P < 0.05* = *, *P < 0.01* = **, *P < 0.001* = ***. Non-significant effects are indicated by 'ns'. *P* values for significant effects are taken from the model output of the MAM in each case, non-significant results are the deletion *P* values from the relevant model simplification, n = 24.

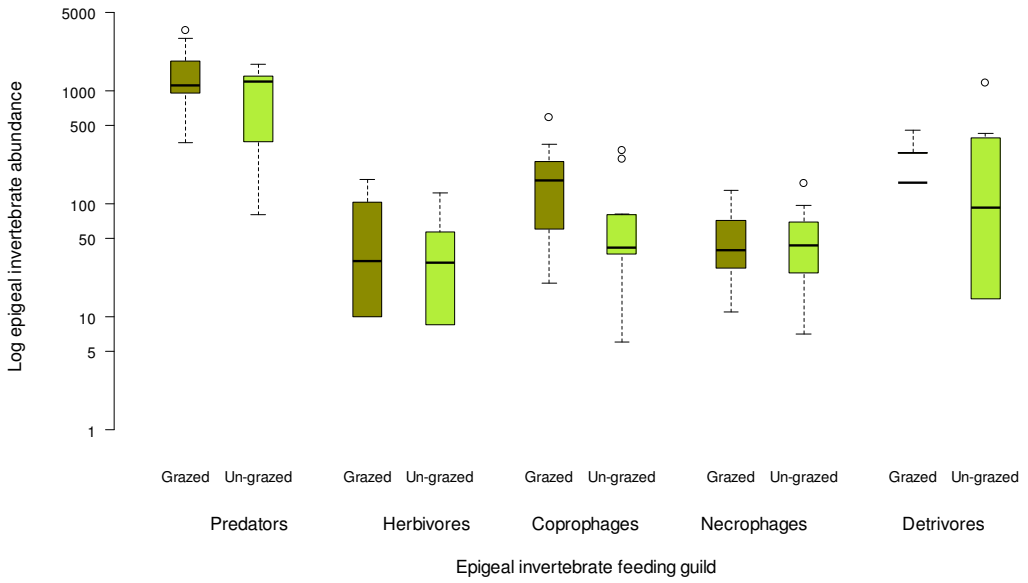


Figure 5. 1 The response of epigeal invertebrate guilds to grazing treatment. No significant difference in the abundance of any of the studied epigeal invertebrate feeding guilds between grazed and un-grazed treatments was detected in the generalised linear models. For statistics see table 5.3. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 5.3. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 24.

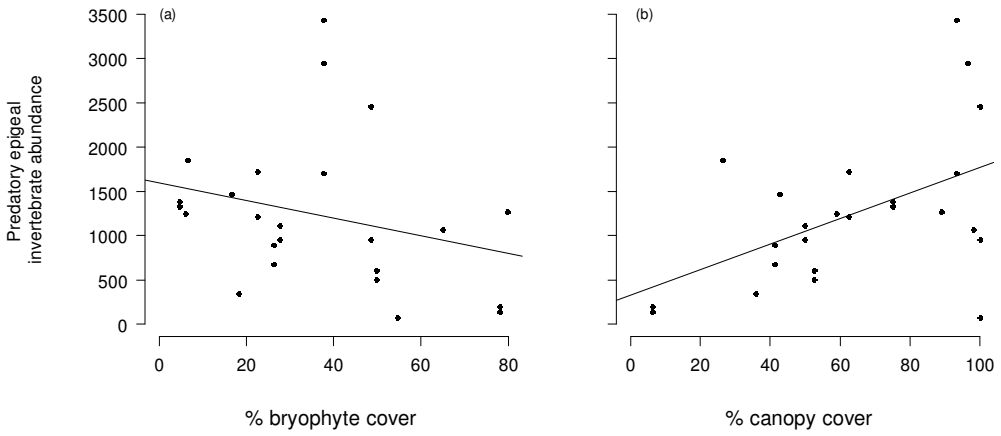


Figure 5. 2 The response of predatory epigeal invertebrate abundance to (a) bryophyte cover and (b) canopy cover. Significant effects of (a) bryophyte cover and (b) canopy cover were detected in the generalised linear model for predatory epigeal invertebrate abundance. Abundance was negatively correlated with bryophyte cover (Estimate = -0.014, SE = 0.006, *t* value = -2.511, P = 0.02, df = 21) and positively correlated with canopy cover (Estimate = 0.017, SE = 0.005, *t* value = 3.508, P = 0.002, df = 21.). Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.2. Lines drawn are regressions of the relationship between the variables, n = 24.

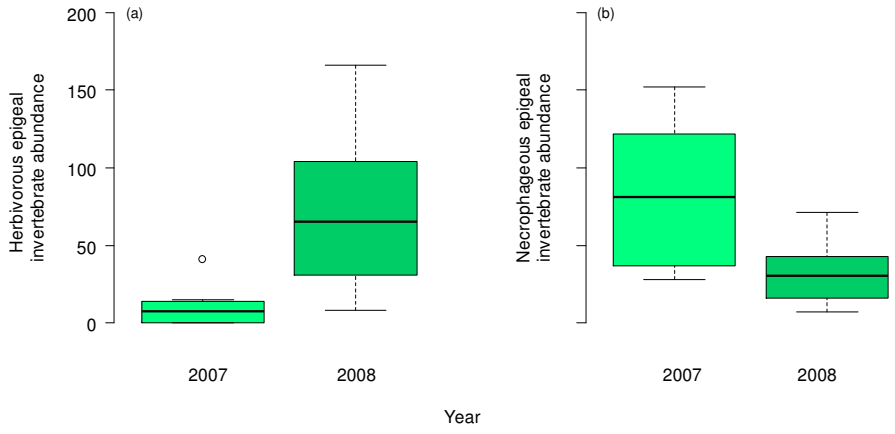


Figure 5. 3 The abundance of (a) herbivorous and (b) necrophagous epigeal invertebrates in 2007 and 2008. Significant effects of year were detected in the generalised linear models for (a) herbivorous and (b) necrophagous epigeal invertebrates. Herbivores were more abundant in 2008 (Estimate = 1.793, SE = 0.364, *t* value = -2.59, P = 0.01, df = 19), and necrophages more abundant in 2009 (Estimate = -0.908, SE = 0.24, *t* value = -3.79, P = 0.001, df = 22). Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 5.2. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 24.

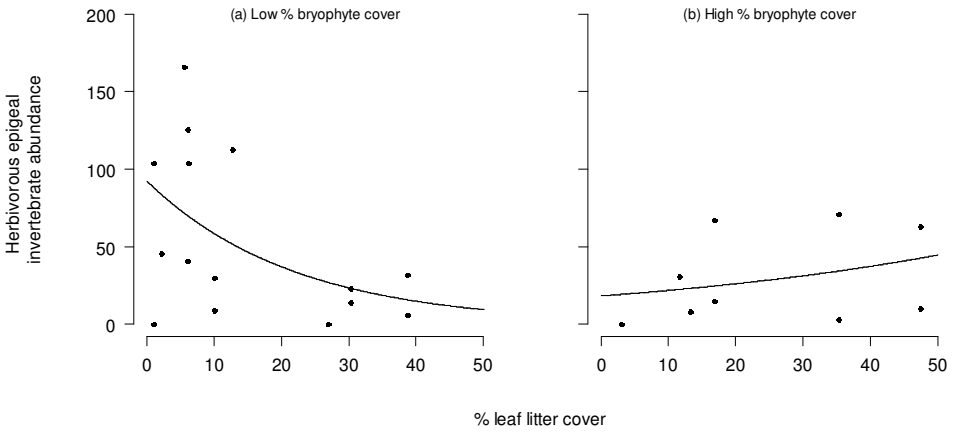


Figure 5. 4 The response of herbivorous epigeal invertebrate abundance to the interaction between leaf litter cover and bryophyte cover. A significant effect of the interaction between bryophyte cover and leaf litter cover was detected in the generalised linear model for herbivorous epigeal invertebrates. Where bryophyte cover was low abundance declined, and where bryophyte cover was high increased in response to increasing leaf litter cover (Estimate = 0.002, SE = 0.001, *t* value = 2.620, P = 0.017, df = 19). Low bryophyte cover ≤ 42.2 %, high bryophyte cover > 42.2 %, determined using the function CUT in R to divide the range of bryophyte cover into two intervals. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.2. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 24.

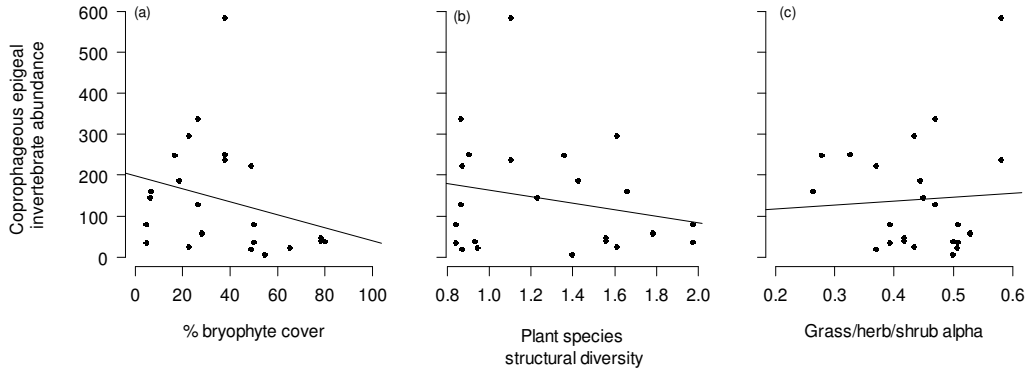


Figure 5. 5 The response of coprophagous epigeal invertebrate abundance to (a) bryophyte cover, (b) plant species structural diversity, and (c) grass/herb/shrub alpha. Significant effects of (a) bryophyte cover, (b) plant species structural diversity and (c) grass/herb/shrub alpha structural diversity were detected in the generalised linear model for coprophagous epigeal invertebrate abundance. Abundance declined in response to increasing bryophyte cover (Estimate = -0.034, SE = 0.011, *t* value = -3.192, P = 0.005, df = 20) and plant species structural diversity (Estimate = -1.204, SE = 0.402, *t* value = -2.994, P = 0.007, df = 20) and increased in response to increasing grass/herb/shrub alpha structural diversity (Estimate = 7.507, SE = 2.388, *t* value = 3.144, P = 0.005, df = 20). Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.2. Lines drawn are regressions of the relationship between the variables, n = 24.

Table 5. 7 Effect sizes and their standard errors of habitat variables on syrphid feeding guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Guild	Estimate	SE	*t* value	*P*		Res. Dev.	df
Microphages							
Intercept	4.435	1.756	2.525	0.045	*	1117.2	6
Tree/shrub species richness	-0.768	0.249	-3.081	0.022	*		
Herb species richness	1.640	0.545	3.009	0.024	*		
Grass-herb species ratio	7.542	0.771	9.777	< 0.001	***		
Grass-herb-shrub-alpha	14.891	3.989	3.733	0.010	**		
Tree/shrub species richness : grass-herb species ratio	-6.139	0.647	-9.491	< 0.001	***		
Grass-herb-shrub alpha : tree/shrub species diversity	10.919	0.983	11.112	< 0.001	***		
Herb species richness : Grass-herb-shrub alpha	-5.946	1.270	-4.683	0.003	**		
Herbivores							
Intercept	14.060	1.411	9.968	< 0.001	***	92281	10
Plant species structural diversity	-1.425	0.734	-1.941	0.081	.		
Overall plant diversity	-5.236	2.258	-2.318	0.043	*		
Plant species structural diversity : Overall plant diversity	3.039	1.191	2.552	0.029	*		
Saproxylic							
Intercept	7.517	0.800	9.401	0.000	***	60935	12
Plant height diversity	1.259	0.530	2.377	0.035			
Predators							
Intercept	10.951	0.522	20.980	< 0.001	***	280181	12
Grass-herb-shrub alpha	2.755	1.125	2.449	0.031	*		

Notes: Note: Asterisks indicate the level of significance: *P < 0.05 = *, P < 0.01 = **, P < 0.001 = ****. Non-significant effects are indicated by 'ns', n = 14.

Table 5. 8 Non-significant grazing exclosure treatment effects on syrphid feeding guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. P: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Guild	Estimate	SE	*t* value	*P*		Res. Dev.	df
Microphages							
Intercept	0.090	0.292	0.307	0.764	ns	8.582	12
Grazing (un-grazed)	0.470	0.396	1.188	0.258	ns		
Herbivores							
Intercept	2.241	0.163	13.753	< 0.001	***	25.422	12
Grazing (un-grazed)	0.096	0.242	0.396	0.699	ns		
Saproxylic							
Intercept	2.978	0.148	20.184	< 0.001	***	42.288	12
Grazing (un-grazed)	-0.011	0.226	-0.049	0.961	ns		
Predators							
Intercept	-0.288	0.330	-0.871	0.401	ns	7.704	12
Grazing (un-grazed)	0.651	0.430	1.512	0.156	ns		

Notes: Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***. Non-significant effects are indicated by 'ns'. *P* values for significant effects are taken from the model output of the MAM in each case, non-significant results are the deletion *P* values from the relevant model simplification, n = 14.

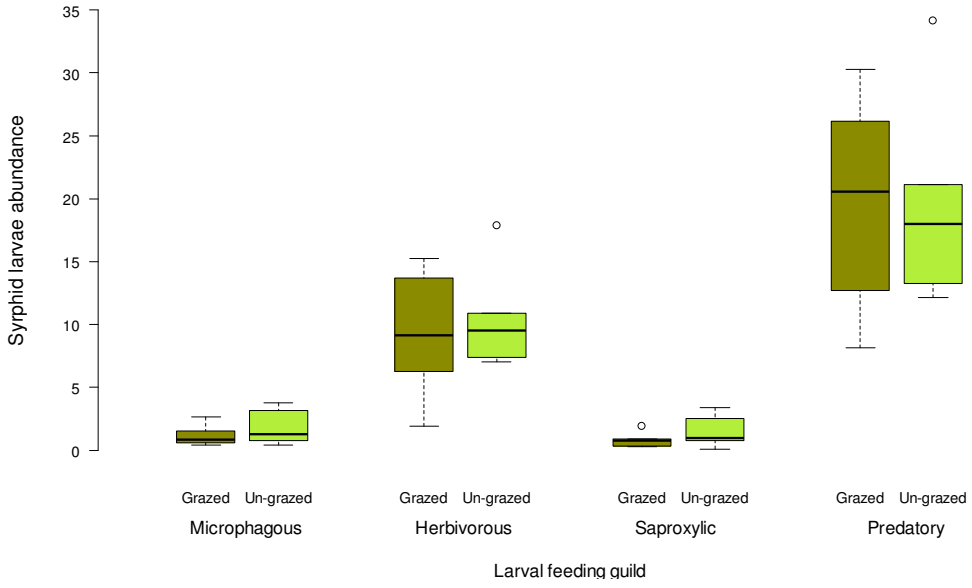


Figure 5. 6 The response of adult hoverfly whose larvae are (a) microphagous, (b) phytophagous, (c) saproxylic and (d) predatory, to grazing. No significant difference in the abundance of any of the studied syrphid feeding guilds between grazed and un-grazed treatments was detected in the generalised linear models. For statistics see table 5.5. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 5.5. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 14.

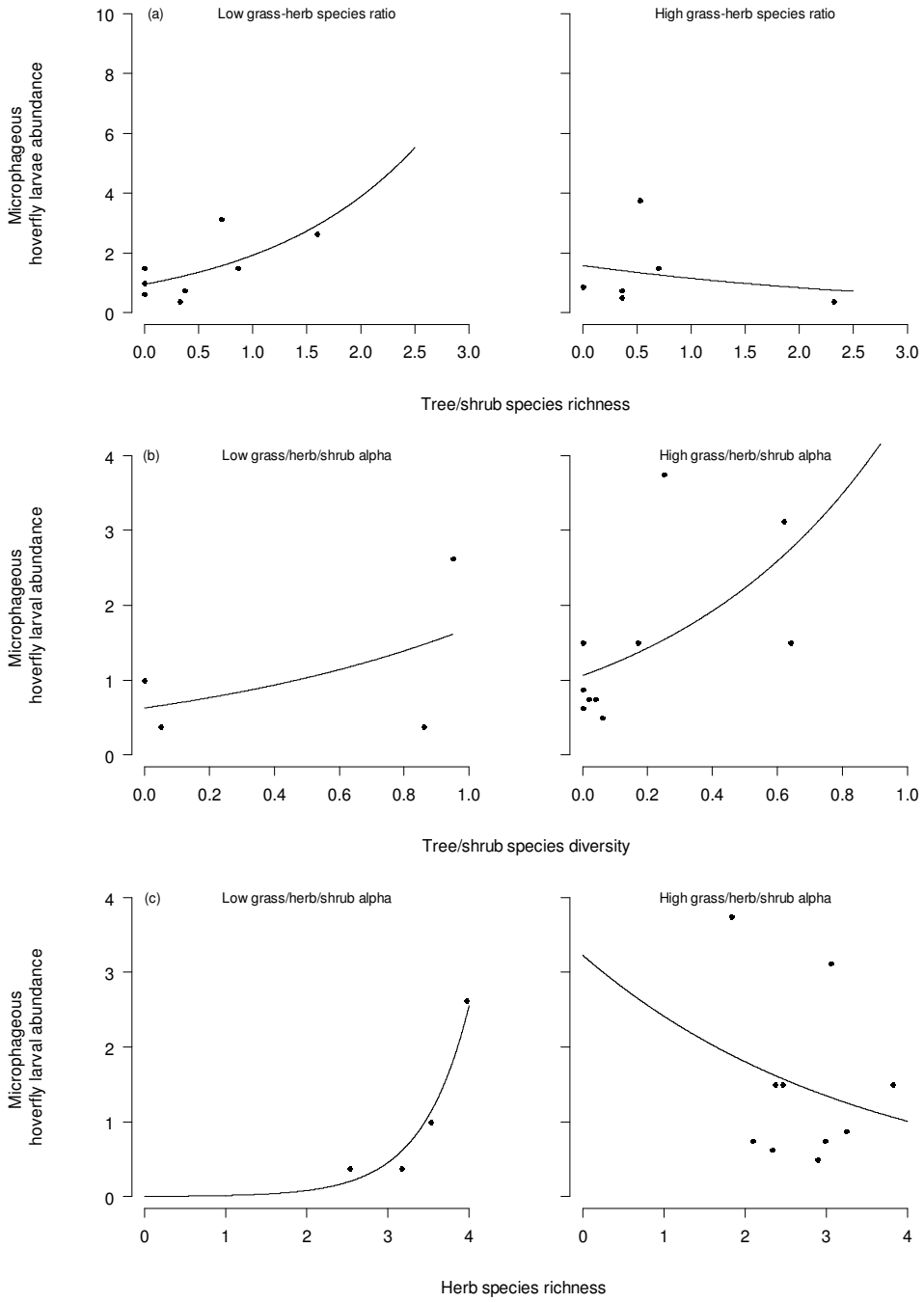


Figure 5. 7 The response of the abundance of adult hoverflies whose larva are microphagous to the interactions between (a) the grass-herb species ratio and tree-shrub species richness, (b) grass/herb/shrub alpha and tree-shrub species diversity, and (c) the grass-herb species ratio and herb species richness. Significant effects of the interactions between (a) the grass-herb species ratio and tree-shrub species richness, (b) grass/herb/shrub alpha and tree-shrub species diversity, and (c) the grass-herb species ratio and herb species richness were detected in the generalised linear model for adult hoverflies whose larvae are microphagous. Abundance increased were the grass-herb species ratio was low, and increased where the ratio was high, in response to increasing tree/shrub species richness (Estimate = -6.139, SE = 0.647, *t* value = -9.491, P = < 0.001, df = 6), increased slightly where grass/herb/shrub/alpha was low, and more sharply where grass/herb/shrub alpha was high, in response to increasing tree/shrub species diversity (Estimate = 10.919, SE = 0.983, *t* value = 11.112, P = < 0.001, df = 6), and increased steeply where grass/herb/shrub/alpha was low, and declined where grass/herb/shrub alpha was high, in response to herb species richness (Estimate = -5.946, SE = 1.270, *t* value = -4.683, P = 0.003, df = 6). Low grass-herb species ratio ≤ 0.14, high grass-herb species ratio > 0.14, low

grass/herb/shrub alpha ≤ 0.4, high grass/herb/shrub/alpha > 0.4, determined using linear models to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 5.4. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 14.

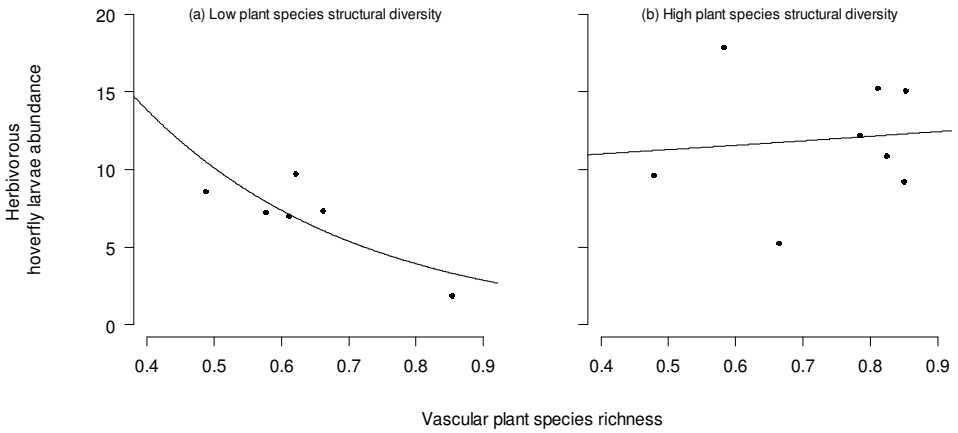


Figure 5. 8 The response of the abundance of adult hoverflies whose larva are herbivorous to the interaction between plant species structural diversity and overall plant species richness. A significant effect of the interaction between plant species structural diversity and vascular plant species richness was detected in the generalised linear model for adult hoverflies whose larvae are herbivorous. Where plant species structural diversity was low abundance declined, and where plant species structural diversity was high increased slightly, in response to vascular plant species richness (Estimate = 3.039, SE = 1.191, *t* value = 2.552, P = 0.029, df = 10). Low plant species structural diversity ≤ 1.1, high plant species structural diversity > 1.1, determined using linear models to identify the value above and below which splitting the variable was most significant. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.4. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 14.

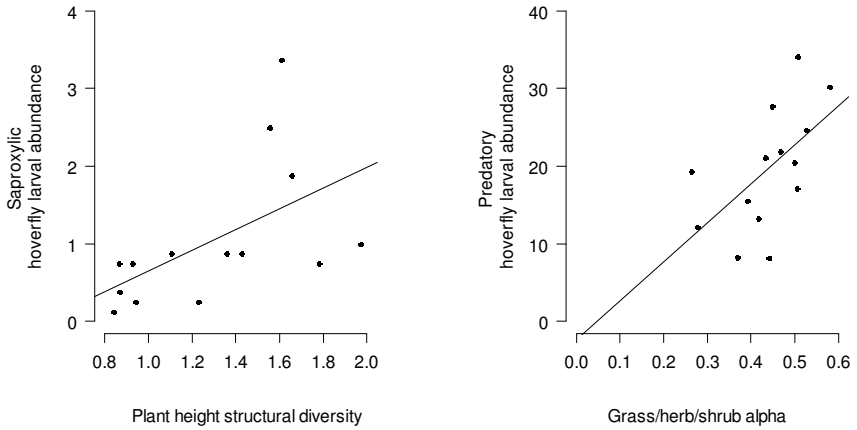


Figure 5. 9 The response of the abundance of adult hoverflies whose larva are (a) saproxyllic to plant height structural diversity, and (b) zoophagous to grass/herb/shrub alpha diversity. Significant effects of plant height structural diversity on the abundance of (a) adult hoverflies whose larvae are saproxylic, and (b) grass/herb/shrub alpha structural diversity on adult hoverflies whose larvae are predatory were detected in the generalised linear models of abundance. In each case abundance increased steeply in response to an increase in the explanatory variable (a) (Estimate = 1.259, SE = 0.530, *t* value = 2.377, P = 0.035, df = 12) (b) (Estimate = 2.755, SE = 1.125, *t* value = 2.449, P = 0.031, df = 12). Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.4. Lines drawn are regressions fitted from the linear model of the relationship between the variables, n = 14.

Table 5. 9 Non-significant grazing exclosure treatment effects on parasitoid guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model *P* value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Guild	Estimate	SE	*t* value	*P*		Res. Dev.	df
Idiobiont							
Intercept	28.906	2.484	11.636	< 0.001	***	10664	54
Grazing (un-grazed)	-4.073	3.795	-1.073	0.288	NS		
Koinobiont							
Intercept	91.031	10.580	8.604	< 0.001	***	193424	54
Grazing (un-grazed)	-5.698	16.161	-0.353	0.726	NS		
Endoparasitic							
Intercept	33.813	3.100	10.906	< 0.001	***	16609	54
Grazing (un-grazed)	-4.063	4.736	-0.858	0.395	NS		
Ectoparasitic							
Intercept	108.340	10.930	9.912	< 0.001	***	206449	54
Grazing (un-grazed)	-11.800	16.700	-0.707	0.483	NS		
Symphytophagous							
Intercept	25.312	4.584	5.522	< 0.001	***	36306	54
Grazing (un-grazed)	-4.646	7.002	-0.664	0.510	NS		
Coleoptrophagous							
Intercept	4.000	0.549	7.292	< 0.001	***	519.96	54
Grazing (un-grazed)	-0.208	0.838	-0.249	0.805	NS		

Notes: Note: Asterisks indicate the level of significance: *P < 0.05 = *, P < 0.01 = **, P < 0.001 = ****. Non-significant effects are indicated by 'ns'. *P* values for significant effects are taken from the model output of the MAM in each case, non-significant results are the deletion *P* values from the relevant model simplification, n = 56.

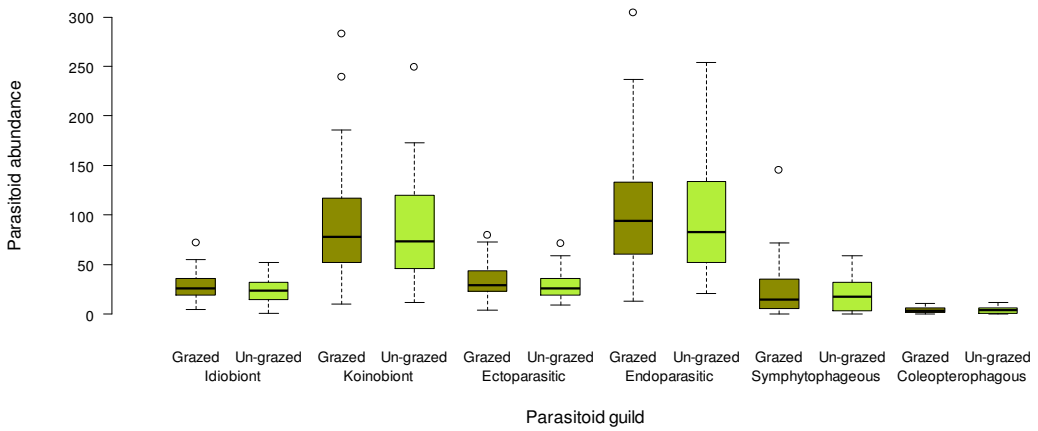


Figure 5. 10 The response of parasitoid guild member abundance to grazing treatment. No significant difference in the abundance of any of the studied parasitoid guilds between grazed and un-grazed treatments was detected in the generalised linear models. For statistics see table 5.6. Note that these figures do not take account of all the factors in the minimal adequate models, but are representative of the general underlying relationships shown in table 5.6. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 56.

Table 5. 10 Effect sizes and their standard errors of habitat variables on idiobiont and koinobiont parasitoid guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Guild	Estimate	SE	*t* value	*P*		Res. Dev.	df
Idiobiont							
Intercept	3.000	0.262	11.462	< 0.001	***	169.16	41
Plant species structural diversity	0.318	0.139	2.293	0.027	*		
May - June	-0.519	0.261	-1.987	0.054	.		
June - July	-0.267	0.242	-1.101	0.277			
July - August	-0.275	0.243	-1.132	0.264			
NVCW17a	-0.245	0.355	-0.690	0.494			
NVCW17c	-1.172	0.953	-1.230	0.226			
Plant species structural diversity : NVC W17a	-0.075	0.176	-0.425	0.673			
Plant species structural diversity : NVC W17c	-0.927	0.381	-2.433	0.019	*		
May - June : NVC W17a	0.501	0.344	1.457	0.153			
June - July : NVC W17a	0.486	0.321	1.513	0.138			
July - August : NVC W17a	0.707	0.316	2.238	0.031	*		
May - June : NVC W17c	2.534	0.910	2.784	0.008	**		
June - July : NVC W17c	3.166	0.876	3.616	0.001	***		
July - August : NVC W17c	2.994	0.880	3.403	0.002	**		
Koinobiont							
Intercept	3.767	0.348	10.829	< 0.001	***	136.06	38
May - June	-0.468	0.246	-1.905	0.064	.		
June - July	-0.208	0.228	-0.912	0.368			
July - August	-0.293	0.229	-1.284	0.207			
Grass/herb/shrub alpha	-1.828	0.857	-2.133	0.039	*		
NVCW17a	-0.281	0.285	-0.987	0.330			
NVCW17c	-2.327	0.781	-2.979	0.005	**		
Plant species structural diversity	0.316	0.091	3.492	0.001	**		
May - June : NVC W17a	0.911	0.400	2.278	0.028	*		
June - July : NVC W17a	0.962	0.376	2.561	0.015	*		
July - August : NVC W17a	0.566	0.372	1.522	0.136			
May - June : NVC W17c	2.704	0.855	3.162	0.003	**		
June - July : NVC W17c	3.368	0.822	4.096	< 0.001	***		
July - August : NVC W17c	2.947	0.824	3.576	0.001	***		
April - May : tree species richness	-0.005	0.203	-0.023	0.982			
May - June : tree species richness	-0.523	0.248	-2.104	0.042	*		
June - July : tree species richness	-0.617	0.230	-2.686	0.011	*		
July - August : tree species richness	0.147	0.168	0.874	0.388			

Notes: Minimal adequate models for (a) idiobiont parasitoid abundance as a function of the interactions between plant species structural diversity and NVC community, and sampling period and NVC community, and (b) koinobiont parasitoid abundance as a function of grass/herb/shrub alpha, plant species structural diversity, and the interactions between sampling period and NVC community, and sampling period and tree species richness. Model simplification for all models follows the same protocol as table 5.2 (a). Models of abundance data are Generalized Linear Models with a quasipoisson error structure. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance. Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***, n = 56.

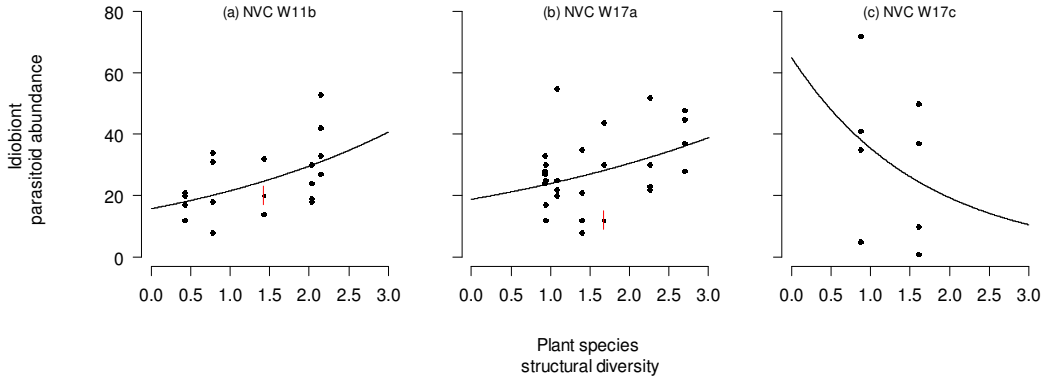


Figure 5. 11 The response of idiobiont parasitoids to plant species structural diversity in each woodland plant community. A significant effect of the interaction between NVC community and plant species structural diversity was detected in the generalised linear model for idiobiont parasitoids. Abundance increased in sub-communities W11b and W17a, and declined in sub-community W17b, in response to plant species structural diversity (Estimate = -0.927, SE = 0.381, *t* value = -2.433, P = 0.019, df = 41). The NVC community factor levels were used to plot graphical representations of the relationships. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.4. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 56.

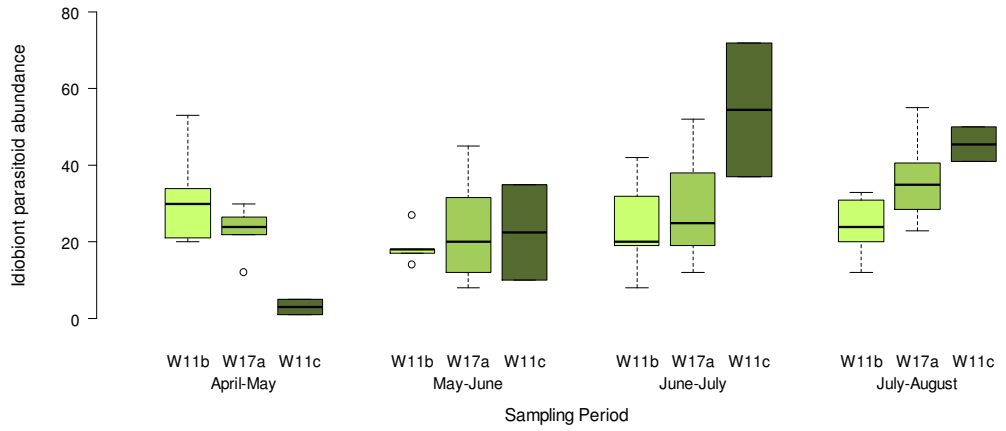


Figure 5. 12 The response of idiobiont parasitoid abundance to the interaction between sample periods and woodland plant community. A significant effect of the interaction between sampling period and NVC community was detected in the generalised linear model for idiobiont parasitoid abundance. Idiobiont abundance ~ sample period (July-August) : NVC W17a (Estimate = 0.707, SE = 0.316, *t* value = 2.238, *P* = 0.031, df = 41). Idiobiont abundance ~ sample period (May-June) : NVC W17c (Estimate = 2.534, SE = 0.910, *t* value = 2.784, *P* = 0.008, df = 41), Idiobiont abundance ~ sample period (June-July) : NVC W17c (Estimate = 3.166, SE = 0.876, *t* value = 3.616, *P* = 0001, df = 41), Idiobiont abundance ~ sample period (July-August) : NVC W17c (Estimate = 2.994, SE = 0.880, *t* value = 3.403, *P* = 0.002, df = 41).Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations of 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002). See table 5.10 for statistics, n = 56).

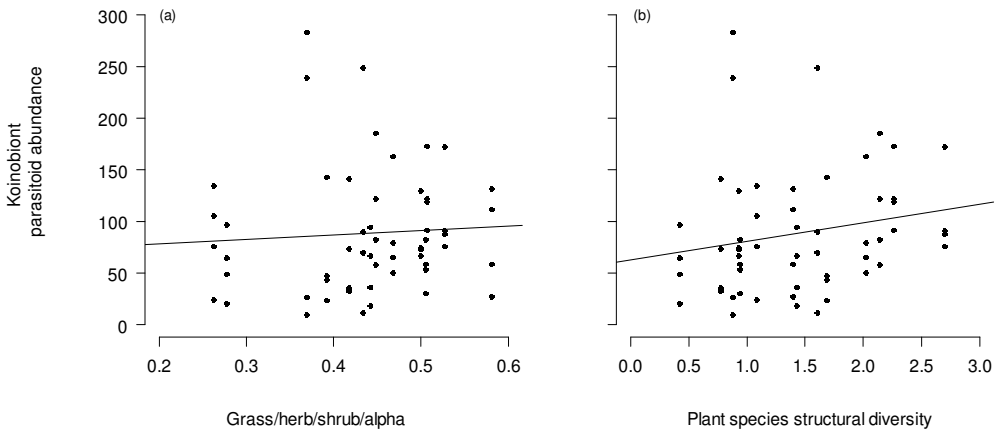


Figure 5. 13 The response of koinobiont parasitoids to (a) grass/herb/shrub alpha diversity and (b) plant species structural diversity. Significant effects of (a) grass/herb/shrub alpha structural diversity and (b) plant species structural diversity were detected in the generalised linear model for koinobiont parasitoid abundance. Abundance increased very slightly in response to increasing grass/herb/shrub alpha (Estimate = -1.828, SE = 0.857, *t* value = -2.133, P = 0.039, df = 38) and more steeply in response to increasing plant species structural diversity (Estimate = 0.318, SE = 0.091, *t* value = 3.492, P = 0.001, df = 38). Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.7. Lines drawn are regressions fitted from the linear model of the relationship between the variables, n = 56.

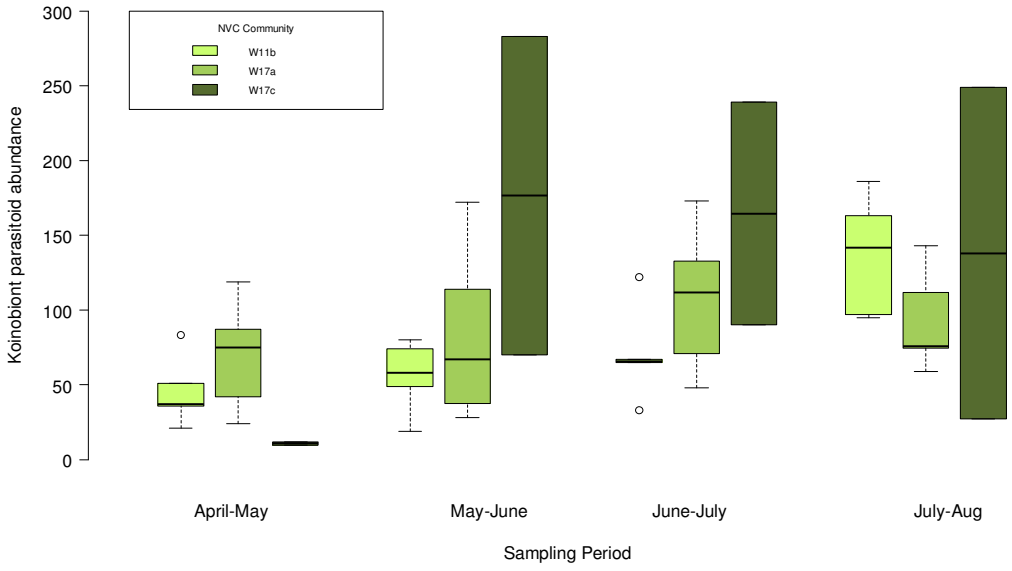


Figure 5. 14 The abundance of koinobiont parasitoids in NVC vegetation communities in each sampling period. A significant effect of the interaction between sampling period and NVC community was detected in the generalised linear model for koinobiont parasitoid abundance. Koinobiont abundance ~ sample period (May-June) : NVC W17c (Estimate = 2.704, SE = 0.855, *t* value = 3.162, *P* = 0.003, df = 38), Koinobiont abundance ~ sample period (June-July) : NVC W17c (Estimate = 3.368, SE = 0.822, *t* value = 4.096, *P* = < 0.001, df = 38), Koinobiont abundance ~ sample period (July-August) : NVC W17c (Estimate = 2.947, SE = 0.824, *t* value = 3.576, *P* = 0.001, df = 38). Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations of 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002), n = 56.

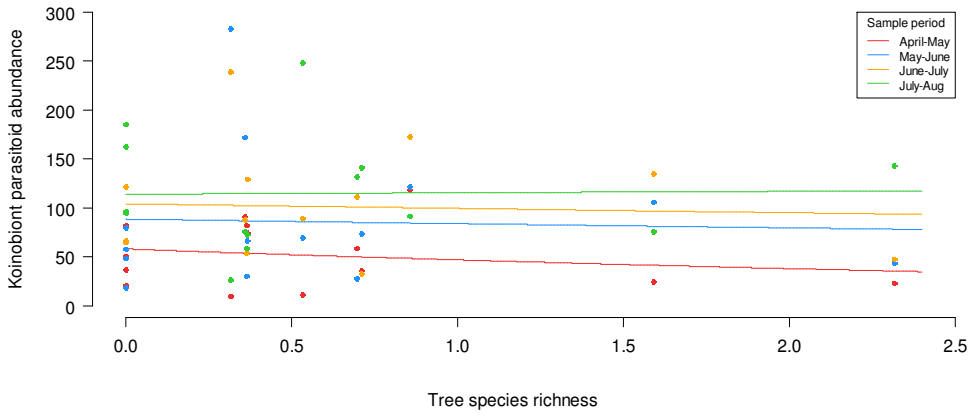


Figure 5. 15 The response of koinobiont parasitoid abundance in (a) April-May, (b) May-June, (c) June-July and (d) July-Aug, to tree species richness. A significant effect of the interaction between sampling period and tree species richness was detected in the generalised linear model for koinobiont parasitoid abundance: Koinobiont abundance ~ sample period (May-June) :tree species richness (Estimate = -0.523, SE = 0.248, *t* value = -2.104, *P* = 0.042, df = 38), Koinobiont abundance ~ sample period (June-July) :tree species richness (Estimate = -0.617, SE = 0.230, *t* value = -2.686, *P* = 0.011, df = 38). Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.4. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 56.

Table 5. 11 Effect sizes and their standard errors of habitat variables on ectoparasitic and endoparasitic parasitoid guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Guild	Estimate	SE	*t* value	*P*		Res. Dev.	df
Ectoparasitic							
Intercept	3.246	0.221	14.699	< 0.001	***	251.89	43
May - June	-0.414	0.283	-1.462	0.151			
June - July	-0.225	0.268	-0.838	0.407			
July - August	-0.084	0.258	-0.325	0.747			
Plant species structural diversity	0.217	0.089	2.422	0.020	*		
NVCW17a	-0.564	0.266	-2.123	0.040	*		
NVCW17c	-1.645	0.678	-2.427	0.019	*		
May - June : NVC W17a	0.596	0.388	1.538	0.131			
June - July : NVC W17a	0.955	0.359	2.663	0.011	*		
July - August : NVC W17a	0.821	0.351	2.338	0.024	*		
May - June : NVC W17c	1.781	0.785	2.269	0.028	*		
June - July : NVC W17c	2.439	0.739	3.301	0.002	**		
July - August : NVC W17c	2.144	0.741	2.895	0.006	**		
Endoparasitic							
Intercept	3.239	0.209	15.466	< 0.001	***	197.3	39
May - June	-0.357	0.268	-1.335	0.190			
June - July	-0.146	0.253	-0.576	0.568			
July - August	-0.092	0.244	-0.378	0.708			
NVCW17a	-0.687	0.321	-2.142	0.039	*		
NVCW17c	-1.692	0.637	-2.656	0.011	*		
Plant species structural diversity	0.208	0.083	2.495	0.017	*		
Tree species richness	0.149	0.232	0.643	0.524			
May - June : NVC W17a	0.965	0.451	2.139	0.039	*		
June - July : NVC W17a	1.475	0.415	3.556	0.001	**		
July - August : NVC W17a	0.767	0.412	1.862	0.070	.		
May - June : NVC W17c	1.930	0.742	2.603	0.013	*		
June - July : NVC W17c	2.665	0.698	3.819	< 0.001	***		
July - August : NVC W17c	2.126	0.697	3.050	0.004	**		
May - June : tree species richness	-0.478	0.348	-1.373	0.178			
June - July : tree species richness	-0.710	0.321	-2.210	0.033	*		
July - August : tree species richness	0.061	0.284	0.216	0.830			

Notes: Notes: Minimal adequate models for (a) ectoparasitic parasitoid abundance as a function of plant species structural diversity and the interaction between NVC community and sampling period, (b) endoparasitic parasitoid abundance as a function of plant species structural diversity, tree species richness, and the interactions between sampling period and NVC community, and sampling period and tree species richness. Model simplification for all models follows the same protocol as table 5.2 (a). See Chapter Two for a full explanation of each of the explanatory variables. Models of abundance data are Generalized Linear Models with a quasipoisson error structure. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance. Asterisks indicate the level of significance: $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***, n = 56.

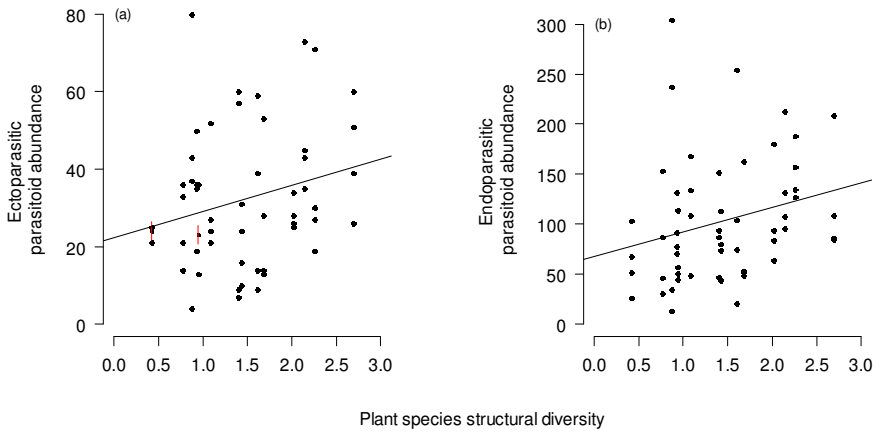


Figure 5. 16 The response of (a) ectoparasitic and (b) endoparasitic parasitoid abundance to plant species structural diversity. Significant effects of plant species structural diversity were detected in the generalise liner models for (a) ectoparasitoid and (b) endoparasitoid abundance. In each case abundance increased in response to increasing plant species structural diversity (a) (Estimate = 0.217, SE = 0.089, *t* value = 2.422, P = 0.020, df = 38) (b) (Estimate = 0.208, SE = 0.083, *t* value = 2.495, P = 0.017, df = 38). Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.8. Lines drawn are regressions fitted from the linear model of the relationship between the variables, n = 56.

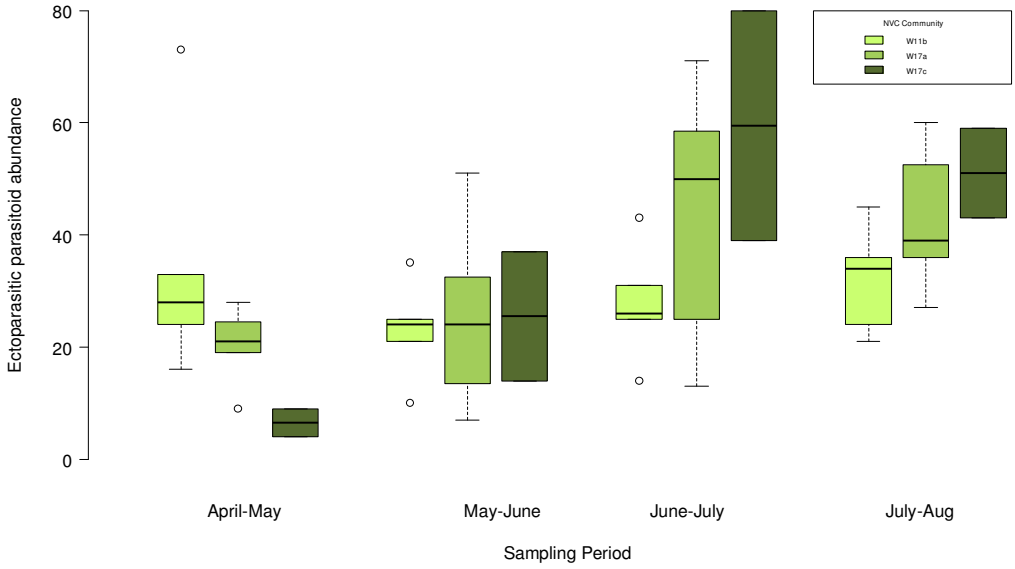


Figure 5. 17 The abundance of ectoparasitic parasitoids in NVC vegetation communities in each sampling period. A significant effect of the interaction between sampling period and NVC community was detected in the generalised linear model for ectoparasitic parasitoid abundance. Ectoparasitic abundance ~ sample period (June-July) :NVC W17a (Estimate = 0.955, SE = 0.359, *t* value = 2.663, *P* = 0.011, df = 43), Ectoparasitic abundance ~ sample period (July-August) :NVC W17a (Estimate = 0.821, SE = 0.351, *t* value = 2338, *P* = 0.024, df = 43), Ectoparasitic abundance ~ sample period (May-June) :NVC W17c (Estimate = 1.781, SE = 0.785, *t* value = 2.296, *P* = 0.028, df = 43), Ectoparasitic abundance ~ sample period (June-July) :NVC W17c (Estimate = 2.439, SE = 0.739, *t* value = 3.301, *P* = 0.002, df = 43), Ectoparasitic abundance ~ sample period (July-August) :NVC W17c (Estimate = 2.144, SE = 0.741, *t* value = 2.895, *P* = 0.006, df = 43). Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations of 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002), n = 56.

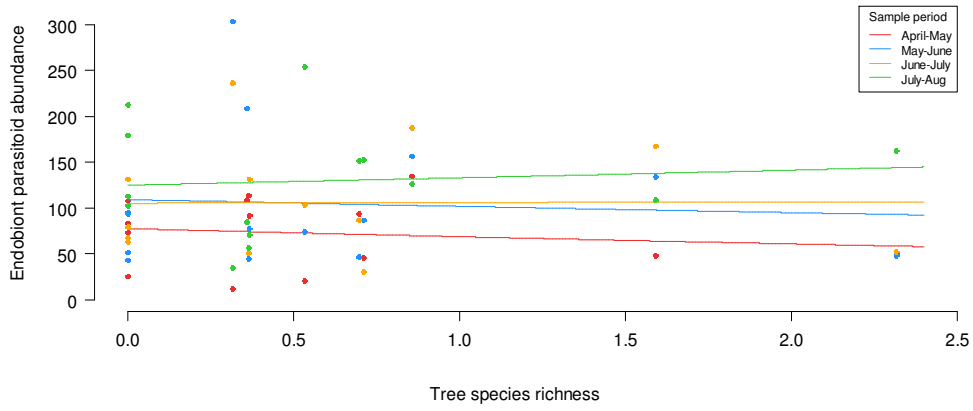


Figure 5. 18 The response of endoparasitic parasitoids to tree species richness in each sampling period. A significant effect of the interaction between sampling period and tree species richness was detected in the generalised linear model for endobiont parasitoid abundance. Endoparasitic abundance ~ sample period (June-July) : tree species richness (Estimate = -0.710, SE = 0.321, *t* value = -2.210, *P* = 0.033, df = 43) The sampling period factor levels were used to plot graphical representations of the relationships. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.8. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 56.

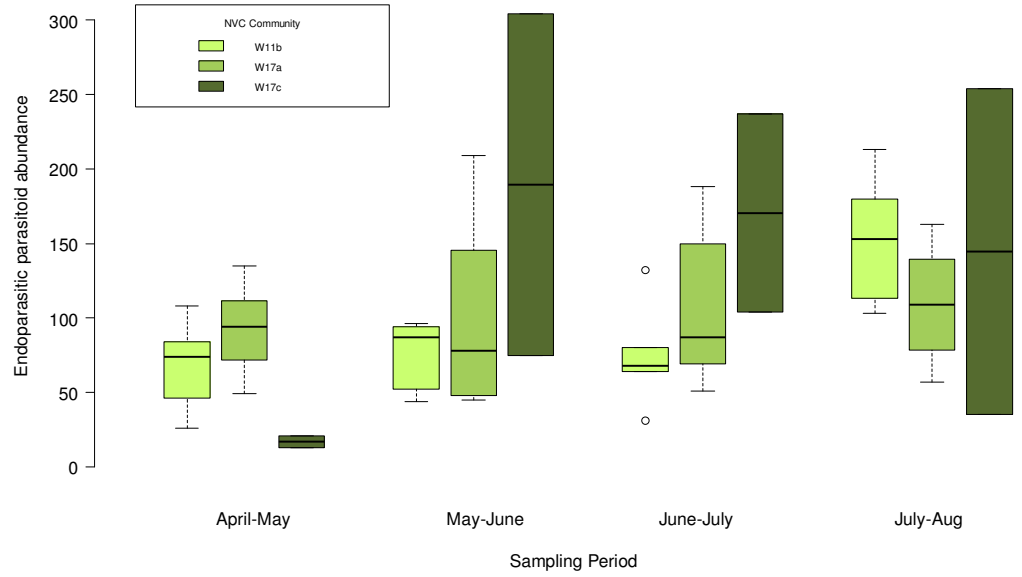


Figure 5. 19 The abundance of endoparasitoids in NVC vegetation communities in each sampling period. A significant effect of the interaction between sampling period and NVC vegetation community was detected in the generalised linear model for endoparasitic parasitoid abundance. Endoparasitic abundance ~ sample period (May-June) : NVC W17a (Estimate = 0.965, SE = 0.451, *t* value = 2.139, *P* = 0.039, df = 43), Endoparasitic abundance ~ sample period (June-July) : NVC W17a (Estimate = 1475, SE = 0.415, *t* value = 3.556, *P* = 0.001, df = 43), Endoparasitic abundance ~ sample period (May-June) : NVC W17c (Estimate = 1.930, SE = 0.742, *t* value = 2.603, *P* = 0.013, df = 43), Endoparasitic abundance ~ sample period (June-July) : NVC W17c (Estimate = 2.665, SE = 0.698, *t* value = 3.819, *P* = < 0.001, df = 43), Endoparasitic abundance ~ sample period (July-August) : NVC W17c (Estimate = 2.126, SE = 0.697, *t* value = 3.050, *P* = 0.004, df = 43). Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations of 1.5 times the interquartile range of the data, whichever is the smaller (Crawley, 2002), n = 56.

Table 5. 12 Effect sizes and their standard errors of habitat variables on coleoptrophagous and symphytophagous parasitoid guilds. Estimate: estimate of the model slope, indicating the change in response per unit increase of the explanatory variable. SE: standard error of the model estimate. t value: model t statistic. *P*: model P value. df: degrees of freedom. Res. Dev.: Residual Deviance.

Guild	Estimate	SE	*t* value	*P*		Res. Dev.	df
Coleopterophagous							
Intercept	1.384	1.565	0.884	0.382		86.93	43
Grass/herb/shrub alpha	7.092	2.456	2.888	0.006	**		
May - June	0.599	2.085	0.287	0.775			
June - July	-0.056	1.983	-0.028	0.978			
July - August	0.478	1.918	0.249	0.804			
Vascular plant diversity	-5.001	1.503	-3.327	0.002	**		
Grazing (un-grazed)	0.010	0.186	0.056	0.956			
Grass/herb/shrub alpha : May - June	-10.298	3.489	-2.951	0.005	**		
Grass/herb/shrub alpha : June - July	-6.150	3.129	-1.965	0.056	.		
Grass/herb/shrub alpha : July - August	-9.129	3.104	-2.941	0.005	**		
May - June : vascular plant species diversity	5.466	2.271	2.407	0.020	*		
June - July : vascular plant species diversity	4.623	1.986	2.328	0.025	*		
July - August : vascular plant species diversity	5.742	1.978	2.903	0.006	**		
Symphytophagous							
Intercept	-8.584	3.283	-2.615	0.012	*	695.26	49
May - June	1.880	0.523	3.593	0.001	***		
June - July	1.935	0.522	3.709	0.001	***		
July - August	1.833	0.525	3.492	0.001	**		
Vascular plant diversity	12.305	4.072	3.022	0.004	**		
Vegetation height diversity	5.097	2.012	2.533	0.015	*		
Vascular plant diversity : vegetation height diversity	-5.926	2.666	-2.223	0.031	*		

Notes: Note: Asterisks indicate the level of significance: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***. Non-significant effects are indicated by 'ns'. P values for significant effects are taken from the model output of the MAM in each case, n = 56.

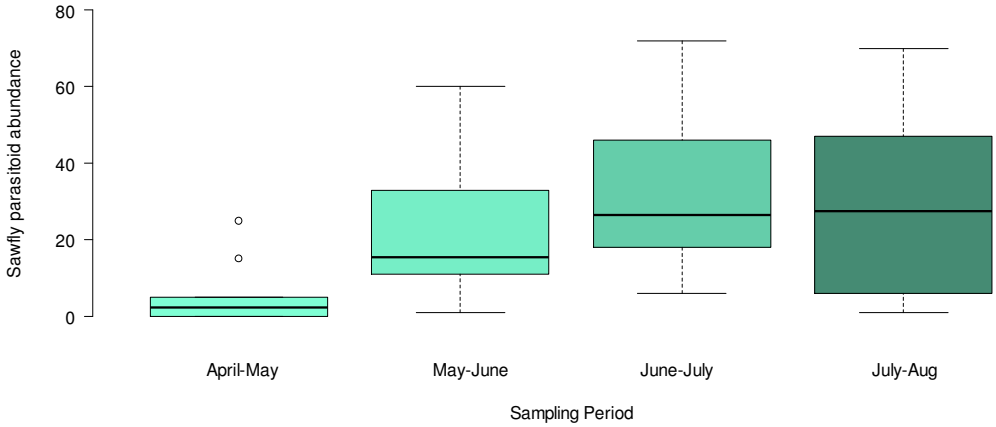


Figure 5. 20 The response of symphytopagous parasitoid abundance to sampling period. A significant effect of sampling period was detected in the generalised linear model for symphytopagous parasitoid abundance. Abundance was significantly higher in May-June (Estimate = 1.880, SE = 0.523, *t* value = 3.593, P = 0.001, df = 49) June-July (Estimate = 1.935, SE = 0.522, *t* value = 3.709, P = 0.001, df = 0.001) and July-August (Estimate = 1.833, SE = 0.525, *t* value = 3.492, P = 0.001, df = 49) than in April-May (Estimate = -8.584, SE = 3.283, *t* value = -2.615, P = 0.012, df = 49). The sampling period factor levels were used to plot graphical representations of the relationships. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.8. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002), n = 56.

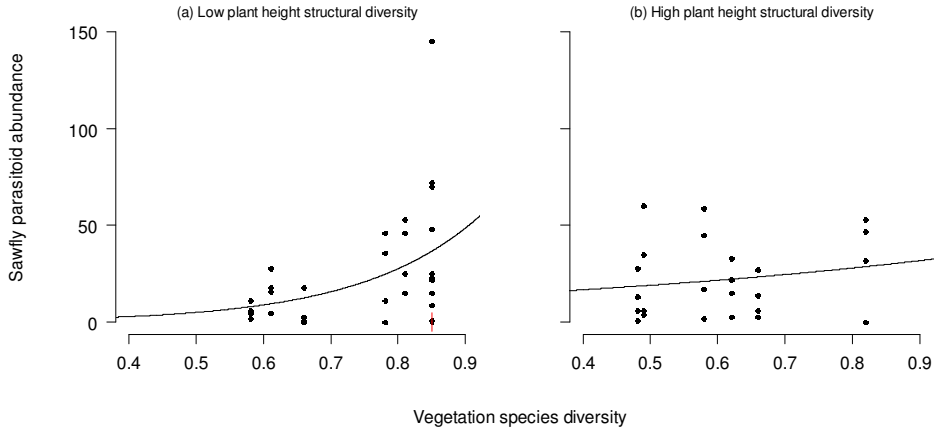


Figure 5. 21 The response of sawfly parasitoid abundance to the interaction between vascular plant species diversity and plant height structural diversity. A significant effect of the interaction between plant height structural diversity and vascular plant species diversity was detected in the generalised linear model for symphytophagous parasitoid abundance. Where plant height structural diversity was low abundance began to increase exponentially, and where plant height structural diversity was high increased gently, in response to vascular plant species diversity (Estimate = -5.296, SE = 2.666, *t* value = -2.233, P = 0.031, df = 49). Low plant height structural diversity ≤ 1.41, high plant height structural diversity > 1.41, determined using linear models to identify the value above and below which splitting the variable was most significant, determined using the function CUT in R to divide the range of plant height structural diversity into two intervals. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.9. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 56.

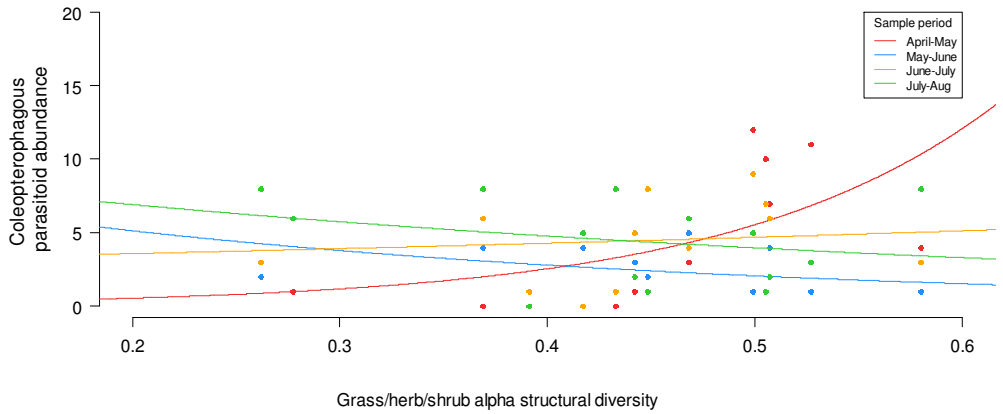


Figure 5. 22 The response of Coleoptera parasitoid abundance to grass/herb/shrub alpha structural diversity during each sampling period. A significant effect of the interaction between sampling period and grass/herb/shrub alpha structural diversity was detected in the generalised linear model for coleopterophagous parasitoid abundance. Coleoptrophagous parasitoid abundance ~ grass/herb/shrub alpha : sample period (May-June) : Estimate = -10.298, SE = 3.489, *t* value = 2.951, *P* = 0.005, Coleoptrophagous parasitoid abundance ~ grass/herb/shrub alpha : sample period (July-August) : Estimate = -9.129, SE = 3.104, *t* value = -2.941, *P* = 0.005, df = 43. The sampling period factor levels were used to plot graphical representations of the relationships. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.9. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 56.

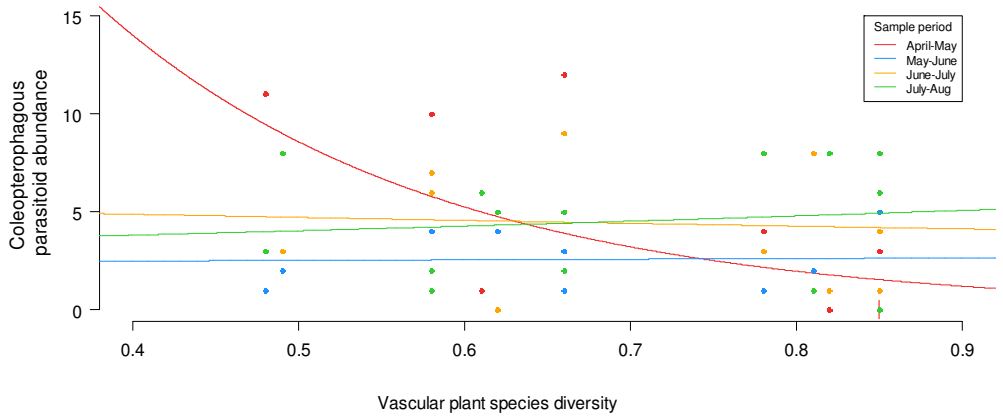


Figure 5. 23 The response of Coleoptera parasitoid abundance to vascular plant species diversity in each sampling period. A significant effect of the interaction between sampling period and vascular plant species diversity was detected in the generalised linear model for coleopterophagous parasitoid abundance. Coleoptrophagous parasitoid abundance ~ sample period (May-June) : vascular plant species diversity: Estimate = 5.466, SE = 2.271, *t* value = 2.407, *P* = 0.020, Coleoptrophagous parasitoid abundance ~ sample period (June-July) : vascular plant species diversity: Estimate = 4.623, SE = 1.986, *t* value = 2.328, *P* = 0.025, Coleoptrophagous parasitoid abundance ~ sample period (July-August) : vascular plant species diversity: Estimate = 5.742, SE = 1.978, *t* value = 2.903, *P* = 0.006, df = 43. The sampling period factor levels were used to plot graphical representations of the relationships. Note that these figures do not take account of all the factors in the minimal adequate model, but are representative of the general underlying relationships shown in table 5.9. Lines are drawn using information from the fitted model to produce smooth functions to plot a line through the scatter plot (Crawley, 2002). Model is a GLM with quasipoisson errors, therefore negative values are not predicted, n = 56.

5.3.8 Dung removal

There was not a significant effect of grazing treatment on the removal of dung from experimental pellet groups. Significantly more dung was removed from treatments from which Geotrupids were not excluded than those from which they were excluded (figure 5.24c). The amount of dung removed was also positively correlated with vegetation structural complexity (figure 5.24a), and the abundance of Geotrupid beetles (figure 5.24b).

Table 5. 13 Effect sizes and their standard errors of the minimal adequate model of factors affecting the amount of dung removed from experimental pellet group exclusion treatments.

Variable	Estimate	SE	*t* value	*P*		Res. Dev.	df
Intercept	100.293	17.579	5.705	< 0.001	***	13122	24
Vegetation structural complexity	26.942	12.052	2.235	0.035	*		
Exclusion treatment	19.904	8.838	2.252	0.034	*		
Geotrupid spp. abundance	0.147	0.058	2.560	0.017	*		

Notes: Minimal adequate model for the amount of dung removed from experimental pellet group exclusion treatments as a function of vegetation structural complexity (α diversity index of herb layer plant structures in height categories in a vertical plane), exclusion treatment (a categorical variable with two levels, Geotrupids either excluded or not from the experimental pellet group), and the abundance of Geotrupid beetles in each woodland plot. Explanatory variables excluded during model simplification included grazing treatment (grazed or un-grazed), plot size, plot age (length of grazing exclusion), deer density, vegetation structural complexity measured as the diversity of the grass-herb-shrub gradient, and all of the two-level interaction terms. Asterisks indicate the level of significance: *P < 0.05* = *, *P < 0.01* = **, *P < 0.001* = ***, n = 28.

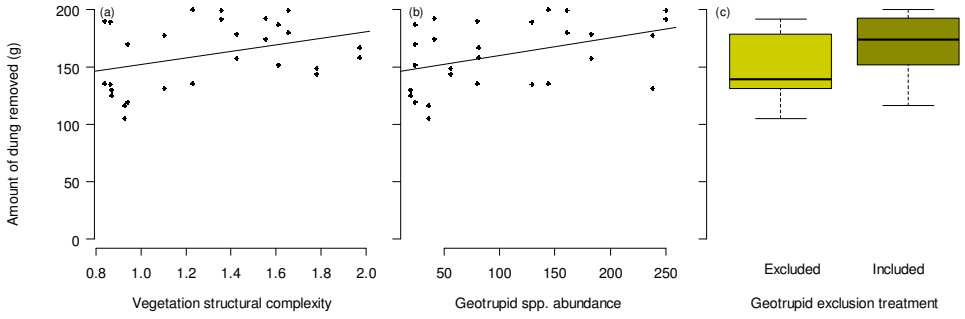


Figure 5. 24 The amount of dung removed from experimental pellet group exclusion treatments in response to (a) vegetation structural complexity, (b) Geotrupid spp. abundance, and (c) exclusion treatment.
The amount of dung removed was positively correlated with vegetation structural complexity (t = 2.235, P = 0.035, df = 24), and the abundance of Geotrupid beetles (t = 2.560, P = 0.017, df = 24). Significantly more dung was removed from treatments from which Geotrupids were not excluded than those from which they were excluded (t = 2.252, P = 0.034, df = 24). The lines drawn are regression lines fitted from the linear model of the relationship. Boxes show the interquartile range with the median shown as a bold line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is smaller (Crawley, 2002). Note that these figures do not take into account all the factors in the full model shown in table 6.3, but are representative of the general underlying relationships, n = 28.

5.5 Discussion

Considering the differences in vegetation between grazed and un-grazed treatments, it is very surprising that there were no significant effects of fencing on the abundance of any of the studied invertebrate guilds. This lack of response may either be the result of a number of ecological factors, or a consequence of the limitations of the experiment. Using the guild concept in this study allowed examination of groups of interacting and competing species that use the same ecological resources and have similar functional roles (Simberloff and Dayan, 1991, Voigt *et al.*, 2007). The advantages of this approach complement that taken in Chapter Four, where it was impossible to study all species simultaneously.

If not grazing, what did affect guild structure in the Letterewe oak woodland? Effects of vegetation species composition were observed, the general trend being one of increasing guild member abundance in response to vegetation species richness, diversity and structural characteristics, independent of fencing treatment. The reduced heterogeneity, both in structural and species compositional terms, of grazed vegetation is often implicated as the cause of a decrease in the abundance of secondary consumers, due to a corresponding decline in niche availability (Cagnolo, 2002, Gibson *et al.*, 1992) and this is applicable to all trophic levels. This is consistent with studies that report greater abundance where vegetation is more complex (Hendrix et al., 1988), however the present study provides no evidence for such an effect of grazing reducing structural heterogeneity to the detriment of invertebrate guilds. Seasonal variation in abundance was observed in four parasitoid guilds, and is most probably a result of increasing prey availability as the season progresses, and the evolution of phenologically driven matching of peak availability and demand.

Were the exclosure plots too small to detect differences between treatments? Experimentally fenced grazing exclosures ranged in size from 2.5 to 14 ha, and grazed plots were contiguous with the entire woodland. Patches of habitat smaller than 2 ha have been considered incapable of supporting populations of invertebrates distinct from surrounding habitats (Levenson, 1981) and for this reason exclosures smaller than 2.5 ha were not used in this study. This resulted in a mean fenced exclosure size of 6.9 ha. Many invertebrates are highly mobile and active, and it can be argued that relatively small exclosure plots are of a size insufficient to detected habitat preferences over the spatial scale of the experiment, due to the mobility of invertebrates that simply don't recognise the boundaries of such patches. This argument is rejected on several counts. Firstly, the most compelling evidence against this spatial scale verses mobility argument is manifest in the results of Chapter Four, in which significant effects over the same spatial scale were observed on invertebrate abundance,

richness and diversity. Plots more abundant in prey might be expected to be more abundant in their predators, for instance coleopterophagous parasitoids. No such effect was observed, suggesting that this guild was not affected, despite the effect on its prey. Secondly, despite their mobility, invertebrates show preferences or association with habitat features at small spatial scales, and local abundance of individuals will be reflected accordingly in trap catches. Hoverfly trap catches are reported to respond significantly to small scale changes in environmental variables (Dziock, 2006), which is probably reflective of the requirements of many syrphids on patchy and ephemeral resources such as nectar and oviposition microsites. Thirdly, while parasitoids are generally highly mobile and strong flyers, many of their hosts are very closely associated with vegetation and other habitat structures. Idiobiont and ectoparasitic parasitoids collected in this study belonged largely to sub-families that prey on hosts concealed within living plant tissue, dead wood, and bracket fungi. The koinobiont and endoparasitic parasitoids collected are predators of weakly or non-concealed hosts that are mainly herbivorous. Some parasitoids locate hosts through chemical signals emitted by plants in response to herbivore feeding damage, hosts may be rendered toxic to parasitoids through absorption of secondary plant metabolites, and adults require diapause and roosting sites such as tussocks or dense vegetation (Shaw, 2006). Despite such close association of hosts with vegetation, and a significant grazing effect on vegetation, no effect on parasitoid guilds was observed. Thus the grazing effects on vegetation have the potential to profoundly influence the suitability of those habitats for parasitoids and result in correspondingly abundant trap catches irrespective of mobility. These factors, in conjunction with mean exclosure size, are considered reasonable grounds for assuming the experiment was conducted at an appropriate spatial scale to detect grazing effects on guilds.

Are ground dwelling invertebrates un-affected by the vegetation above them? In the case of the epigeal invertebrate guilds, a case could be made that the vegetation above the epiagic layer, despite the significant differences observed between treatments, will not impact animals living below it, as they do not directly come into contact with it, feed on it, or its herbivores. Subsequently it may be argued that no matter how different the variation in the grazed and un-grazed vegetation, ground dwelling invertebrates will be unaffected. There are a number of factors that are important in determining epigeal invertebrate densities that relate to the conditions created by the vegetation that make it unlikely that this argument be given merit. Epigeal invertebrates in common with many others, require specific microclimatic conditions as their small body size renders them more susceptible to fluctuations in moisture and temperature levels than larger organisms (Gullan and Cranston, 2000). Temperature,

moisture levels, light penetration and wind velocity at the epiagic layer are all altered by the structure of vegetation, and as such vegetation plays an important role in determining the suitability of the habitat for its inhabitants. Greater structural complexity of the vegetation will provide a greater biomass and apparency of plant structures on which herbivores and their predators feed. The availability of oviposition sites will increase, microclimatic conditions become more favourable to many invertebrates through increased moisture retention in the epigeal and understory layers, wind energy is dispersed more effectively, and denser vegetation affords a greater degree of protection from solar radiation, all important limiting factors to invertebrates that have limited control of their thermoregulation and moisture retention capabilities. There are a suite of other factors that may vary over a structural heterogeneity gradient that may also be important in determining species and guild level abundance, including symbiosis, nurse plant effects, seed dispersal, availability of breeding sites and entire habitats. Grazing can have either a positive or negative effect on plant species composition, and therefore a corresponding effect on those resources provided by those species. Significant responses to vegetation were observed in the epigeal coprophages with two measures of structural complexity, and several parasitoid guilds to structural and species compositional variables. This clearly demonstrates the potential for these classical postulated mechanisms to impact invertebrates, and the independence of their effect to grazing on guild member abundance in the Letterewe experiment. Given the distinct differences in vegetation, and the more sessile habits of many prey species associated with it (i.e. Lepidoptera and Sawfly larvae, predated by many parasitoids, and aphids, predated by many syrphid larvae), I am particularly confident in accepting that the observed pattern of predatory guild distribution is one unaffected by grazing, rather than one undetectable at the spatial scale of the experiment. One aspect of this experiment that may not yet be apparent in guild response is that of temporal effects on the development of vegetation. The oldest exclosures had been in situ for 14 years at the time of the experiment, and despite the dramatic differences between grazed and un-grazed treatments, no effect on guild member abundance was observed. It is very probable that given an increase in the length of time exclosures are in place, for instance over the life span of the oak trees, that more fundamental differences between the treatments will develop, i.e. age of the stand, leading to detectable changes in guild structure.

Were significant effects on individual taxa cancelled out? One disadvantage of the guild approach in this type of study is its inherent lack of species specific resolution of guild member influence on the response, which was addressed in Chapter Four. Almost inevitably

more than one species will exploit a resource, with potentially many 10's of species belonging to the same guild. Across habitat patches they may co-exist harmoniously, exhibit competitive exclusion, or in competition, but all essentially filling the same functional role. It is therefore possible that species level variation in guild member abundance in response to grazing goes undetected when aggregated guild membership is measured. This criticism perhaps requires little attention, as testing this theory would require comprehensive knowledge of every resource utilized by every individual of every species in a guild, and the information gleaned from the guild approach is useful despite this shortcoming.

Red deer are known to transmit up to 88 species of plant seed in their dung (Welch, 1985), and experimental manipulation of the dung feeding guild allowed quantification of the contribution of geotrupid beetles to this ecosystem function. The results suggest that they play a small role in dung removal, but are potentially functionally important. Many dung beetles perform valuable ecosystem services to plants by acting as secondary seed dispersers (Shepherd and Chapman, 1998; Andresen, 2003; Slade et al., 2007; Nichols et al., 2008) and there is much evidence that ungulates act as seed dispersers for plants (Ramos *et al.*, 2006, Shiponeni and Milton, 2006, Bodmer, 1991, Rosas *et al.*, 2008). Despite their small contribution to dung removal, geotrupids may potentially play an important role in the secondary dispersal of seeds, and influence the regulation of plant population dynamics through reduction of density dependent seedling competition, intraspecific competition, and translocation to microsites favoured for germination. Large herbivores have been shown to negatively affect the recovery of vegetation communities where viable alien and non-native plant seeds were more abundant in dung than those of the characteristic vegetation community (Shiponeni and Milton, 2006), and geotrupids may have a negative impact rather than the largely positively influence seen in tropical forest ecosystems (D'Hondt et al., 2008). There was no effect of grazing management through deer exclosures on removal rates, suggesting that dung resource use by coprophages is not impacted by the effects of grazing in this ecosystem under current grazing pressure.

The failings of pitfall trapping are well understood and documented (Woodcock, 2004), and in-depth discussion considered un-necessary here. Considering the consistency of the method used, mitigation of the effects of temporally fluid vegetation structure in the immediate vicinity of traps, and considerable total length of the sampling period, pitfall trapping is considered to be an effective tool in the monitoring of epigeal invertebrates in this study. While large numbers of Malaise traps set in individual woodlands have been shown not to sample the complete parasitoid fauna, using only a few traps in individual woodlands

over short time periods is still considered useful for long-term monitoring (Fraser *et al.*, 2008b). In this study 28 traps were set at the individual woodland scale, and two at the plot scale, over a 5 month period. It is therefore considered that trap replication was adequate to provide useful data in this study. The sampling efficacy of malaise traps may influenced by exact positioning of traps (Saaksjarvi et al., 2006). Rare species may be caught by chance, and strong fliers so may be passing the plot/trap while not being resident. There may also be an effect of shade/sunlight on malaise trap catches. To counter these effects, all traps were located identically with respect to orientation with the sun, and relative abundance was used in comparisons. The methodology used is considered effective in providing representative samples of the fauna associated with treatment plots. The most conspicuous failing of the dung removal experiment was the drying of dung to remove moisture in order to ensure pellet groups were of consistently equal mass. While moisture was quickly regained through precipitation, the attractiveness of dung to coprophages declines quickly with age and moisture loss, such that studies of this type usually use fresh moist dung. In general however, these studies are conducted over relatively short time scales, typically hours, days or weeks (Slade *et al.*, 2007). The long decay time of deer dung, potentially up to 12 months (Mayle, 1999) and observed effect over the five month period of this experiment, are considered reasonable justification for the conclusions drawn. The experiment also did not include a control from which all beetle species were excluded, consequently potential removal of dung by other means could not be quantified. The ratio of mass of dung taken is smaller for rollers (Slade et al., 2007), and may vary with the size of beetle. This study was not able to quantify dung removal relative to the size of beetles, only the abundance of the most common species. The identification and manipulation of a number of functional groups and species, would have allowed me to more finely partition the components of dung removal processes.

5.5.1 Synthesis and applications

Management of grazing through the use of fenced exclosure plots had no effect on guild composition within the Letterewe oak woodland. These results suggest that the continued use of grazing exclosures to facilitate tree regeneration would therefore have no detrimental impact on guild structure over the temporal scale of the experiment. A number of factors were identified as having a positive influence on the abundance of guild members, pertaining in the most part to structural and species compositional elements of the vegetation. This study recommends the maintenance of a gradient of vegetation heterogeneity and a mosaic of habitat patches, through the continued use of grazing exclosures to facilitate oak

regeneration, and grazing by red deer to regulate plant community composition. This study does not provide any evidence that removing deer altogether would be either beneficial or detrimental to invertebrate guild members, although it is possible that increased numbers of deer could have a detrimental effect if their population were to reach levels associated with overgrazing, thereby reducing vegetation structural heterogeneity. This is unlikely to occur in a food limited population regulated by stalking in such a way as to target those animals that would naturally be selected by the now absent predatory species, and in habitat managed for conservation priorities. The absence of an effect of grazing management on the abundance of secondary consumers diminishes the possibility of herbivore population explosions that have the potential to alter ecosystem stability and sustainability.

5.6 Conclusions

The lack of a grazing effect on the abundance of any of the 16 guilds examined, despite significant variation in vegetation, suggests that across the trophic range, through primary, secondary, tertiary consumers and detritivores, management of red deer through the use of grazing exclosures is not a significant determinant of guild member abundance at the spatial scale of the Letterewe grazing exclosures, and guild coverage examined here. The main trends of grazing and vegetation variability effects on guild member abundance are consistent across all trophic levels. These results indicate that the management practise of using small scale grazing exclosures on a rotational basis in conjunction with grazed habitat patches is consistent with the maintenance of invertebrate guild structure and conservation in the Letterewe oak woodland. This study also demonstrates the potentially important role of geotrupid dung beetles in providing ecosystem services in red deer grazed habitats, with particular reference to secondary seed dispersal.

Chapter 6

General Discussion

6.1 Summary of findings

The effects of grazing on biodiversity by large ungulates have been well studied, although to date most of this work has focused on domestic livestock, rather than wild animals. In this study the consequences of two wild red deer grazing management strategies, in two habitat types, were examined for a range of invertebrate responses. The results of this thesis strongly indicate that for many species, groups and guilds of invertebrates, red deer grazing can have positive effects on biodiversity.

In Chapter Three, comparison of high and low grazing pressure in heather moorland highlights the benefit of extensive grazing by a food limited deer population, compared to that prevailing under a heavy culling policy, for a variety of invertebrate groups. Chapter Four demonstrates the consequences for invertebrate biodiversity of complete exclusion of grazing in oak woodland, with consistently similar results across a range of taxa. The anticipated effect mediated by the dramatic differences in vegetation between treatments was only subtle, and typically grazed treatments had higher invertebrate biodiversity than exclosure. No evidence of a detrimental effect of grazing compared to exclusion was observed. These results strongly indicate that grazing by red deer can be integral to a management plan that seeks to maintain biodiversity in Atlantic oak woodland and are consistent with other evidence (Olff and Ritchie, 1998, Rambo and Faeth, 1999). The examination of functional guilds in Chapter Five complemented the approach taken in Chapter Four, allowing grazing effects on groups of competing species to be quantified. Considering the variation in vegetation between grazing treatments, and the effects observed in Chapter Four, it was surprising that there was no evidence of a grazing effect on any of the 16 guilds examined. The results of Chapters Four and Five strongly suggest that when compared to exclusion, grazing by red deer has positive, and has had no detrimental impact on biodiversity and guild structure over the temporal scale of the experiment.

Throughout this thesis, a number of factors were identified as being positively associated with invertebrate biodiversity and guild member abundance, pertaining in the most part to structural and botanical species composition of vegetation. Habitat management is important in determining vegetation structure and the effect of grazing on vegetation and invertebrate communities have important consequences for conservation and management of other taxa. The observed variation in response of invertebrates to habitat parameters is reflective of the highly complex nature of the interactions between grazing, habitat and inhabitants, and supportive of the widely postulated theories relating to mosaics of habitat patches and their support of biodiversity (Sroka and Finch, 2006, Ings and Hartley, 1999). Based on this and other evidence, taking a blanket approach of simply increasing vegetation biomass through reducing grazer density, with its perceived benefits to biodiversity, would seem to have little merit in the habitats studied here. More preferable should be the approach of creating and maintaining a diversity of patches within habitats. The use of traditional moorland management practices such as burning, as well as grazing, help to maintain a diverse mosaic, and stimulate new heather growth and drive floral and faunal diversity.

This study recommends that the continued use of grazing exclosures to facilitate tree regeneration, and the regulation of vegetation dynamics by red deer, provide the best compromise by which woodland preservation, its continued use by deer for grazing and shelter, and invertebrate biodiversity maintenance can be achieved. More widely, strong evidence is presented to suggest that a deer population of a size consistent with viable deer stalking opportunities can be seen as integral and not contradictory to, conservation in the Scottish Highlands. Heather moorland is after all an anthropogenic landscape, and such activities are integral to the natural heritage and biodiversity that conservationists aim to protect. This is especially true where deer populations are maintained in a quasi-natural dynamic, by stalking carried out in such a way as to fill the ecological role of the now absent top carnivores. These findings have potentially important consequences not only for the intrinsic value of invertebrate diversity in heather moorland, but also particularly the fortunes of moorland bird species, many of which depend largely or wholly on an invertebrate diet, and a considerable number of which are subjects of conservation concern. Extensive grazing at Letterewe was associated with higher invertebrate biodiversity than was observed under the higher cull level at Beinn Eighe, or complete exclusion in oak woodland. The potential implications of these findings are highly consequential for deer stalking estates throughout the Highlands and beyond. The extent of the conflict of interest between conservation bodies and estate management can be reduced if feasible commercial stalking densities are not as

damaging as perceived, or in fact are beneficial to biodiversity. Development of these findings may lead to a more harmonious relationship between stakeholders, who may currently be taking conflicting approaches towards the same overall goal. The key findings of this thesis are in agreement with a large number of previous studies. There is however also a large body of contradictory work. This illustrates that studies such as this are required to determine the effects of grazing and browsing in specific habitats and in individual circumstances in order to develop and inform management and conservation policy. This work clearly demonstrates that a blanket approach with regard to the effects of grazing and browsing may not always be appropriate for the maximisation of biodiversity priorities.

6.2 General limitations

Probably the most obvious limitation of this work is the number of independent samples and the consequences for interpretation of the results. Chapter Three was an observational study of two grazing extremes, based on two moorland estates. This represents an effective sample size of 1, at which much criticism can be directed. In large scale landscape studies such as this, the ideal scenario would be to replicate the pairs, or a gradient of grazing treatments widely throughout the Highlands. In this study this was limited both by remit and practical considerations, however similar studies focused on as few as two moorlands have proved useful in other instances (Hartley, 2003).

Chapter Three highlights the limitations of the family rather than species level approach. This may go some way to explaining why the Lepidoptera, identified to species, were the only group that did not conform to trend. It is possible that this approach to other groups may reveal similar affects on diversity, independent of abundance. This would also have facilitated identification of specific host plants allowing greater degree of speculation as to the mechanisms driving community composition.

The concept of reducing grazing pressure is addressed in Chapter Five, and although not possible in the time frame of this study, is an interesting thought experiment. Conversely it was not possible to test the effects of increasing deer numbers. It may be that grazing pressure at Letterewe is below the threshold at which biodiversity is maximised, and that a higher density would have further gains. The benefits of reducing deer numbers to natural tree regeneration are clear, but not complicit with the entire suite of stakeholder objectives. Increasing deer numbers is possible through targeted management and reduced culling pressure, and would provide the opportunity to test for an effect. Since this would be in conflict with some stakeholder objectives, and current deer densities support a viable stalking

enterprise and higher biodiversity than lower densities, one could suggest that this is an irrelevant argument.

6.3 Further work

To address the main limitation of this study, landscape scale crossed factorial experiments are the logical progression of this work, and would allow inclusion of a range of deer densities in models of grazing impacts. In order to make the these findings applicable and practical to the vast number of deer habitat managers, the development a suite of indicator taxa and non-technical parameters that can be quantified quickly and economically in order to determine the effects of herbivores in specific habitats and under specific grazing and browsing pressure is necessary. Protocols for rapid biodiversity assessment have been successfully developed for a variety of applications and are equally applicable here (Oliver and Beattie, 1996).

Obviously due to the nature of this study, only invertebrates and to some extent plants, have been examined, although much can be inferred from the results. The impacts of red deer grazing on the plant communities at Letterewe was examined in considerable detail by Milner *et al.,* (2002) although there is much scope for the study of mosses, liverworts and lichens and their responses to grazing management, especially considering their intrinsic nature in Atlantic oak woodland.

The results of the experimental manipulation of coprophagy highlight the potentially important role of this functional process for secondary seed dispersal, and especially the particular lack of empirical evidence relating to temperate ecosystems. This work should be viewed as a catalyst for further investigation of this under explored area of temperate ecology.

There are many interesting questions to be asked of the nature of vertebrate interactions with grazing management, particularly in relation to small mammals and birds. Birds are of particular interest due to their charismatic nature and popularity with the general public, often acting as flagship species, and being indicative of the general 'health' of biodiversity. Many species are insectivorous, and many that are not are dependent upon invertebrates as adults, require invertebrate food for their offspring. There are a wide variety of trophic exploitation and niche use characteristics that may be subject to grazing impacts. Variation in food availability, particularly invertebrates as shown here, nesting sites and vegetation characteristics are all important factors affecting the ecology of birds, and equally so mammals, and would benefit from examination with relation to grazing effects. While some empirical research in this area has been reported (Allombert *et al.*, 2005a, Baines, 1996,

Evans *et al.*, 2005, Evans *et al.*, 2006b, Fuller, 2001, Vandenberghe *et al.*, 2009), as with invertebrates there is a paucity of data relating to red deer grazing. The Glen Finglas experiment in central Scotland has produced evidence of effects on foraging behaviour, breeding abundance, egg size and the abundance of arthropod components of moorland bird diets, of domestic livestock grazing regimes (Evans *et al.*, 2005, Evans *et al.*, 2006b, Vandenberghe *et al.*, 2009, Dennis *et al.*, 2008). This system provides a model both of the potential for red deer grazing effects, and of a suitable experimental protocol.

6.4 Conclusion

Concern over the detrimental impacts of grazing due to increasing deer numbers has lead to conflicting objectives between conservation and deer managers. Despite significant variation in deer grazing pressure and vegetation, the abundance of invertebrates between grazed and un-grazed, and heavily and lightly grazed habitat, the anticipated effect of red deer grazing pressure was only important in determining two aspects of the Lepidoptera assemblage. Much positive evidence and very little negative evidence for impacts of grazing is evident. This work highlights the need for science to inform land management policy that must often seek to balance conservation objectives with economic interests, and supports the notion that a red deer herd of a size consistent with viable stalking interests can be integral to the maintenance of heather moorland and oak woodland biodiversity and the natural heritage.

References

Abensperg Traun, M. (1996) The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet Eucalyptus salubris woodland in the Western Australian wheatbelt .1. Arthropods. *The Journal of applied ecology,* **33,** 1281-1301.

Albrecht, M., Schmid, B., Obrist, M., Schupbach, B., Kleijn, D. & Duelli, P. (2010) Effects of ecological compensation meadows on arthropod diversity in adjacent intensively managed grassland. *Biological Conservation,* **143,** 642-649.

Allombert, S., Gaston, A.J. & Martin, J.L. (2005a) A natural experiment on the impact of overabundant deer on songbird populations. *Biological Conservation,* **126,** 1-13.

Allombert, S., Stockton, S. & Martin, J.L. (2005b) A natural experiment on the impact of overabundant deer on forest invertebrates. *Conservation Biology,* **19,** 1917-1929.

Alonso, C. & Herrera, C.M. (1996) Variation in Herbivory within and among Plants of Daphne Laureola (Thymelaeaceae): Correlation with Plant Size and Architecture. *Journal of ecology,* **84,** 495-502.

Altesor, A., Pineiro, G., Lezama, F., Jackson, R.B., Sarasola, M. & Paruelo, J.M. (2006) Ecosystem changes associated with grazing in subhumid South American grasslands. *Journal of Vegetation Science,* **17,** 323-332.

Andresen, E. & Laurance, S.G.W. (2007) Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. *Biotropica,* **39,** 141-146.

Baines, D. (1996) The implications of grazing and predator management on the habitats and breeding success of black grouse Tetrao tetrix. *The Journal of applied ecology,* **33,** 54-62.

Baines, D., Sage, R.B. & Baines, M.M. (1994) The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *The Journal of applied ecology,* **31,** 776-783.

Bardgett, R.D., Marsden, J.H. & Howard, D.C. (1995) The Extent and Condition of Heather on Moorland in the Uplands of England and Wales. *Biological Conservation,* **71,** 155-161.

Bartlett, R., Pickering, J., Gauld, I. & Windsor, D. (1999) Estimating global biodiversity: tropical beetles and wasps send different signals. *Ecological Entomology,* **24,** 118-121.

Basset, Y., Mavoungou, J., Mikissa, J., Missa, O., Miller, S. & Kitching, R. (2004) Discriminatory power of different arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests. *Biodiversity and conservation,* **13,** 709-732.

Bell, J.R., Wheater, C., Phillip.A & Cullen, W.R. (2001) The implications of grassland and heathland management for the conservation of spider communities: a review. *Journal of zoology,* **255,** 377-387.

Blamey, M. & Grey-Wilson, C. (2003) *Cassel's Wild Flowers of Britain and Northern Europe.* Cassel, London.

Blondel, J. (2003) Guilds or functional groups: does it matter? *Oikos,* **100,** 223-231.

Bodmer, R. (1991) Strategies of seed dispersal and seed predation in Amazonian ungulates *Biotropica,* **23,** 255-261.

Bokdam, J. & Gleichman, J.M. (2000) Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology,* **37,** 415-431.

Botes, A., McGeoch, M.A. & van Rensburg, B.J. (2006) Elephant- and human-induced changes to dung beetle (Coleoptera : Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biological Conservation,* **130,** 573-583.

Buchanan, G.M. (2006) The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *The Ibis,* **148,** 615-628.

Buchanan, G.M., Grant, M.C., Sanderson, R.A. & Pearce-Higgins, J.W. (2006) The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis,* **148,** 615-628.

Bullock, J.M. & Pakeman, R.J. (1997) Grazing of lowland heath in England: Management methods and their effects on heathland vegetation. *Biological Conservation,* **79,** 1-13.

Burgio, G. & Sommaggio, D. (2007) Syrphids as landscape bioindicators in Italian agroecosystems. *Agriculture Ecosystems & Environment,* **120,** 416-422.

Butterfield, J., Luff, M.L., Baines, M. & Eyre, M.D. (1995) Carabid beetle communities as indicators of conservation potential in upland forests. *Forest ecology and management,* **79,** 63-77.

Cagnolo, L. (2002) Diversity and guild structure of insect assemblages under grazing and exclusion regimes in a montane grassland from Central Argentina. *Biodiversity and conservation,* **11,** 407-420.

Chen, B. & Wise, D. (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology,* **80,** 761-772.

Cloyd, R. & Sadof, C. (2000) Effects of plant architecture on the attack rate of Leptomastix dactylopii (Hymenoptera : Encyrtidae), a parasitoid of the citrus mealybug (Homoptera : Pseudococcidae). *Environmental Entomology,* **29,** 535-541.

Clutton-Brock, T.H., Coulson, T. & Milner, J. (2004a) Red deer stocks in the Highlands of Scotland. *Nature,* **429,** 261-262.

Clutton-Brock, T.H., Coulson, T. & Milner, J.M. (2004b) Red deer stocks in the Highlands of Scotland. *Nature,* **429,** 261-262.

Cole, L.J. (2002) Relationships between agricultural management and ecological groups of ground beetles (Coleoptera : Carabidae) on Scottish farmland. *Agriculture, ecosystems & environment,* **93,** 323-336.

Cole, L.J., Pollock, M.L., Robertson, D., Holland, J.P. & McCracken, D.I. (2006) Carabid (Coleoptera) assemblages in the Scottish uplands: the influence of sheep grazing on ecological structure. *Entomologica Fennica,* **17,** 229-240.

Coll, M. & Bottrell, D.G. (1996) Movement of an insect parasitoid in simple and diverse plant assemblages. *Ecological Entomology,* **21,** 141-149.

Cote, S.D. (2004) Ecological impacts of deer overabundance. *Annual review of ecology, evolution, and systematics,* **35,** 113-147.

Crawley, M.J. (1983) *Herbivory. The dynamics of Animal-Plant Interactions.* Blackwell Scientific Publications, Oxford.

Crawley, M.J. (2002) *Statistical Computing. An introduction to Data Analysis using S-plus.* Wiley, Chichester, England.

Crawley, M.J. (2007) *The R Book.* John Wiley and Sons Ltd, Chichester.

Crist, T., Pradhan-Devare, S. & Summerville, K. (2006) Spatial variation in insect community and species responses to habitat loss and plant community composition. *Oecologia,* **147,** 510-521.

D'Hondt, B., Bossuyt, B., Hoffmann, M. & Bonte, D. (2008) Dung beetles as secondary seed dispersers in a temperate grassland. *Basic and applied ecology,* **9,** 542-549.

Den Herder, M., Virtanen, R. & Roininen, H. (2004) Effects of reindeer browsing on tundra willow and its associated insect herbivores. *The Journal of applied ecology,* **41,** 870-879.

Dennis, P. (2004) Consequences for biodiversity of reducing inputs to upland temperate pastures: effects on beetles (Coleoptera) of cessation of nitrogen fertilizer application and reductions in stocking rates of sheep. *Grass and forage science,* **59,** 121-135.

Dennis, P., Skartveit, J., McCracken, D.I., Pakeman, R.J., Beaton, K., Kunaver, A. & Evans, D.M. (2008) The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology,* **45,** 279-287.

Dennis, P., Young, M.R. & Gordon, I.J. (1998) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological entomology,* **23,** 253-264.

Dennis, P., Young, M.R., Howard, C.L. & Gordon, I.L. (1997) The response of epigeal beetles (Col: Carabidae, Staphylinidae) to varied grazing regimes on upland Nardus stricta grasslands. *The Journal of applied ecology,* **34,** 433-443.

Di Giulio, M., Edwards, P.J. & Meister, E. (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology,* **38,** 310-319.

Dodgshon, R.A. & Olsson, G.A. (2006) Heather moorland in the Scottish Highlands: the history of a cultural landscape, 1600-1880. *Journal of Historical Geography,* **32,** 21-37.

Duncan, A.J., Hartley, S.E., Thurlow, M., Young, S. & Staines, B.W. (2001) Clonal variation in monoterpene concentrations in Sitka spruce (Picea sitchensis) saplings and its effect on their susceptibility to browsing damage by red deer (Cervus elaphus). *Forest Ecology and Management,* **148,** 259-269.

Dziock, F. (2006) Life-history data in bioindication procedures, using the example of hoverflies (Diptera, syrphidae) in the Elbe floodplain. *International review of hydrobiology,* **91,** 341-363.

Ebeling, A., Klein, A., Schumacher, J., Weisser, W. & Tscharntke, T. (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos,* **117,** 1808-1815.

Edwards, G.R. & Crawley, M.J. (1999) Effects of disturbance and rabbit grazing on seedling recruitment of six mesic grassland species. *Seed Science Research,* **9,** 145-156.

Evans, D.M., Redpath, S.M., Elston, D.A., Evans, S.A., Mitchell, R.J. & Dennis, P. (2006a) To graze or not to graze? Sheep, voles, forestry and nature conservation in the British uplands. *Journal of Applied Ecology,* **43,** 499-505.

Evans, D.M., Redpath, S.M., Evans, S.A., Elston, D.A. & Dennis, P. (2005) Livestock grazing affects the egg size of an insectivorous passerine. *Biology Letters,* **1,** 322-325.

Evans, D.M., Redpath, S.M., Evans, S.A., Elston, D.A., Gardner, C.J., Dennis, P. & Pakeman, R.J. (2006b) Low intensity, mixed livestock grazing improves the breeding abundance of a common insectivorous passerine. *Biology Letters,* **2,** 636-638.

Feber, R.E. (2001) The impacts of deer on woodland butterflies: the good, the bad and the complex. *Forestry,* **74,** 271-276.

Frank, D.A. (2008) Ungulate and topographic control of nitrogen: phosphorus stoichiometry in a temperate grassland; soils, plants and mineralization rates. *Oikos,* **117,** 591-601.
Frank, D.A. & McNaughton, S.J. (1993) Evidence for the Promotion of Aboveground Grassland Production by Native Large Herbivores in Yellowstone-National-Park. *Oecologia,* **96,** 157-161.
Fraser, S., Dytham, C. & Mayhew, P. (2008a) Patterns in the abundance and distribution of ichneumonid parasitoids within and across habitat patches. *Ecological entomology,* **33,** 473-483.
Fraser, S.E.M., Dytham, C. & Mayhew, P.J. (2007) Determinants of parasitoid abundance and diversity in woodland habitats. *Journal of Applied Ecology,* **44,** 352-361.
Fraser, S.E.M., Dytham, C. & Mayhew, P.J. (2008b) The effectiveness and optimal use of Malaise traps for monitoring parasitoid wasps. *Insect Conservation and Diversity,* **1,** 22-31.
Fukumoto, H. & Kajimura, H. (2001) Guild structures of seed insects in relation to acorn development in two oak species. *Ecological research,* **16,** 145-155.
Fuller, R.J. (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. *Forestry,* **74,** 289-298.
Fuller, R.J. & Gough, S.J. (1999) Changes in sheep numbers in Britain: implications for bird populations. *Biological Conservation,* **91,** 73-89.
Gamito, S. (2010) Caution is needed when applying Margalef diversity index. *Ecological Indicators,* **10,** 550-551.
Gardner, S.M. (1991) Ground beetle (Coleoptera, Carabidae) communities on upland heath and their association with heathland flora. *Journal of biogeography,* **18,** 281-289.
Gardner, S.M., Hartley, S.E., Davies, A. & Palmer, S.C.F. (1997) Carabid communities on heather moorlands in northeast Scotland: The consequences of grazing pressure for community diversity. *Biological conservation,* **81,** 275-286.
Gauld, I. & Bolton, B. (1988) *The Hymenoptera.* Oxford University Press, Oxford.
Gebert, C. & Verheyden - Tixier, H. (2001) Variations of diet composition of Red Deer (Cervus elaphus L.) in Europe. *Mammal Review,* **31,** 189-201.
Gibson, C.W.D. (1992a) Changes in spider (Araneae) assemblages in relation to succession and grazing management *The Journal of applied ecology,* **29,** 132-142.
Gibson, C.W.D. (1992b) The response of invertebrate assemblies to grazing *Ecography,* **15,** 166-176.
Gibson, C.W.D., Brown, V.K., Losito, L. & McGavin, G.C. (1992) The Response of Invertebrate Assemblies to Grazing. *Ecography,* **15,** 166-176.
Gimingham, C. (1985a) Age-related interactions between Calluna vulgaris and phytophagous insects. *Oikos,* **44,** 12-16.
Gimingham, C.H. (1985b) Age-Related Interactions between Calluna-Vulgaris and Phytophagous Insects. *Oikos,* **44,** 12-16.
Gittings, T., O'Halloran, J., Kelly, T. & Giller, P. (2006) The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. *Forest ecology and management,* **237,** 290-300.
Godfray, H.C.J. (1994) *Parasitoids-Behavioural and Evolutionary Ecology.* Princeton University Press, Princeton, New Jersey.
Godin, C. (1999) A method for describing plant architecture which integrates topology and geometry. *Annals of Botany,* **84,** 343.
Gonzalez-Megias, A. (2004) Effects of ungulates on epigeal arthropods in Sierra Nevada National Park (southeast Spain). *Biodiversity and conservation,* **13,** 733-752.

Grant, S.A. & Armstrong, H.M. (1993) Grazing Ecology and the Conservation of Heather Moorland - the Development of Models as Aids to Management. *Biodiversity and Conservation,* **2,** 79-94.

Grant, S.A., Hamilton, W.J. & Souter, C. (1981) The Responses of Heather-Dominated Vegetation in Northeast Scotland to Grazing by Red Deer. *Journal of Ecology,* **69,** 189-204.

Grimbacher, P. & Stork, N. (2007) Vertical stratification of feeding guilds and body size in beetle assemblages from an Australian tropical rainforest. *Austral Ecology,* **32,** 77-85.

Grimbacher, P.S., Catterall, C.P. & Kitching, R.L. (2006) Beetle species' responses suggest that microclimate mediates fragmentation effects in tropical Australian rainforest. *Austral Ecology,* **31,** 458-470.

Grime, J. (1973a) Competitive exclusion in herbaceous vegetation. *Nature,* **242,** 344-347.

Grime, J. (1979) *Plant Strategies and Vegetation Processes.* Boulder: Westview.

Grime, J.P. (1973b) Competitive Exclusion in Herbaceous Vegetation. *Nature,* **242,** 344-347.

Gullan, P.J. & Cranston, P.S. (2000) *The Insects. An Outline of Entomology.* Blackwell Science, Oxford.

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T. & Thies, C. (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *The Journal of applied ecology,* **46,** 1106-1114.

Hanan, J. (2002) Simulation of insect movement with respect to plant architecture and morphogenesis. *Computers and electronics in agriculture,* **35,** 255.

Hanley, N., Davies, A., Angelopoulos, K., Hamilton, A., Ross, A., Tinch, D. & Watson, F. (2008) Economic determinants of biodiversity change over a 400-year period in the Scottish uplands. *Journal of Applied Ecology,* **45,** 1557-1565.

Harrison, K. & Bardgett, R. (2003a) How browsing by red deer impacts on litter decomposition in a native regenerating woodland in the Highlands of Scotland. *Biology and Fertility of Soils,* **38,** 393-399.

Harrison, K.A. & Bardgett, R.D. (2003b) How browsing by red deer impacts on litter decomposition in a native regenerating woodland in the Highlands of Scotland. *Biology and Fertility of Soils,* **38,** 393-399.

Hartley, S.E. (2003) Indirect effects of grazing and nutrient addition on the hemipteran community of heather moorlands. *The Journal of applied ecology,* **40,** 793-803.

Hartley, S.E. & Mitchell, R.J. (2005) Manipulation of nutrients and grazing levels on heather moorland: changes in Calluna dominance and consequences for community composition. *Journal of Ecology,* **93,** 990-1004.

Haslett, J.R. (1989) Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia,* **78,** 433.

Hawkins, B. (1988) Species-diversity in the 3rd and 4th trophic levels - patterns and mechanisms. *The Journal of animal ecology,* **57,** 137-162.

Hawkins, C. & Macmahon, J. (1989) Guilds - the multiple meanings of a concept. *Annual Review of Entomology,* **34,** 423-451.

Haysom, K.A. & Coulson, J.C. (1998) The Lepidoptera fauna associated with Calluna vulgaris: effects of plant architecture on abundance and diversity. *Ecological Entomology,* **23,** 377-385.

Hendrix, S., Brown, V. & Dingle, H. (1988) Arthropod guild structure during early old field succession in a new and old-world site. *The Journal of animal ecology,* **57,** 1053-1065.

Hewson, R. (1976) Grazing by Mountain Hares Lepus-Timidus L, Red Deer Cervus-Elaphus L and Red Grouse Lagopus-L-Scoticus on Heather Moorland in Northeast Scotland. *Journal of Applied Ecology,* **13,** 657-666.

Holden, J., Shotbolt, L., Bonn, A., Burt, T.P., Chapman, P.J., Dougill, A.J., Fraser, E.D.G., Hubacek, K., Irvine, B., Kirkby, M.J., Reed, M.S., Prell, C., Stagl, S., Stringer, L.C., Turner, A. & Worrall, F. (2007) Environmental change in moorland landscapes. *Earth-Science Reviews,* **82,** 75-100.

Hope, D., Picozzi, N., Catt, D.C. & Moss, R. (1996) Effects of reducing sheep grazing in the Scottish Highlands. *Journal of Range Management,* **49,** 301-310.

Hubbard, C.E. (1954) *Grasses.* Penguin Books, London.

Humphrey, J.W., Hawes, C., Peace, A.J., Ferris-Kaan, R. & Jukes, M.R. (1999) Relationships between insect diversity and habitat characteristics in plantation forests. *Forest ecology and management,* **113,** 11-21.

Ings, T. & Hartley, S. (1999) The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. *Forest ecology and management,* **119,** 123-136.

Ings, T.C. (1999) The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. *Forest ecology and management,* **119,** 123-136.

Janzen, D. (1973) Sweep samples of tropical foliage insects - description of study sites, with data on species abundances and size distributions. *Ecology,* **54,** 659-686.

Jessop, L. (1986) *Dung Beetles and Chaffers - Coleoptera: Scarabaeoidea.* The Royal Enntomological Society of London, London.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as Ecosystem Engineers. *Oikos,* **69,** 373-386.

Kareiva, P. & Sahakian, R. (1990) Tritrophic effects of a simple architectural mutation in pea plants. *Nature,* **345,** 433-434.

Kennedy, M. & Gray, R. (1993) Can ecological theory predict the distribution of foraging animals - a critical analysis of experiments on the ideal free distribution. *Oikos,* **68,** 158-166.

Kruess, A. (2002) Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological conservation,* **106,** 293-302.

Kruess, A. & Tscharntke, T. (2002) Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation,* **106,** 293-302.

Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos,* **76,** 5-13.

Lande, R., DeVries, P. & Walla, T. (2000) When species accumulation curves intersect: implications for ranking diversity using small samples. *Oikos,* **89,** 601-605.

Landete-Castillejos, T., Garcia, A., Gomez, J. & Gallego, L. (2003) Lactation under food constraints in Iberian red deer Cervus elaphus hispanicus. *Wildlife Biology,* **9,** 131-139.

Lang, A., Filser, J. & Henschel, J. (1999) Predation by ground beetles and wolf spiders on herbivorous insects in a maize crop. *Agriculture, ecosystems & environment,* **72,** 189-199.

Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters,* **8,** 538-547.

Lawton, J. & Schroder, D. (1977) Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants *Nature,* **265,** 137-140.

Lawton, J.H. (1983) Plant Architecture and the Diversity of Phytophagous Insects. *Annual Review of Entomology,* **28,** 23-39.
Lawton, J.H. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature,* **391,** 72-76.
Levenson, J.B. (1981) *Woodlots as biogeographic islands in Southern Wisconsin.* Springer-Verlag, New York.
Lindroth, C. (1974) *Handbook for the Identification of British Insects, Coleoptera, Carabidae*. Royal Entomological Society of London, London.
Littlewood, N.A. (2006a) Moorland restoration aids the reassembly of associated phytophagous insects. *Biological conservation,* **132,** 395-404.
Littlewood, N.A. (2006b) The response of plant and insect assemblages to the loss of Calluna vulgayis from upland vegetation. *Biological conservation,* **128,** 335-345.
Littlewood, N.A. (2008) Grazing impacts on moth diversity and abundance on a Scottish upland estate. *Insect Conservation and Diversity,* **1,** 151-160.
Loe, L.E., Mysterud, A., Stien, A., Steen, H., Evans, D.M. & Austrheim, G. (2007) Positive short-term effects of sheep grazing on the alpine avifauna. *Biology Letters,* **3,** 109-111.
Luff, M. & Rushton, S. (1989) The ground beetle and spider fauna of managed and unimproved upland pasture. *Agriculture, ecosystems & environment,* **25,** 195-205.
Magurran, A.E. (2004) *Measuring ecological diversity.* Blackwell Publishing., Oxford, UK.
Marrs, R., Phillips, J., Todd, P., Ghorbani, J. & Le Duc, M. (2004) Control of Molinia caerulea on upland moors. *The Journal of applied ecology,* **41,** 398-411.
Marrs, R.H. & Watt, A.S. (2006) Biological Flora of the British Isles: Pteridium aquilinum (L.) Kuhn. *Journal of ecology,* **94,** 1272-1321.
Martin, T.G. & McIntye, S. (2007) Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. *Conservation Biology,* **21,** 504-514.
Martin, T.G. & Possingham, H.P. (2005) Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology,* **42,** 400-408.
Martinsen, G.D., Driebe, E.M. & Whitham, T.G. (1998) Indirect interactions mediated by changing plant chemistry: Beaver browsing benefits beetles. *Ecology,* **79,** 192-200.
Mayle, B.A. (1999) *How many deer? A guide to estimating deer population size.* Forestry Commission.
McEvoy, P.M., Flexen, M. & McAdam, J.H. (2006) The effects of livestock grazing on ground flora in broadleaf woodlands in Northern Ireland. *Forest Ecology and Management,* **225,** 39-50.
McFerran, D.M., Montgomery, W.I. & McAdam, J.H. (1994) The Impact of Grazing on Communities of Ground-Dwelling Spiders (Araneae) in Upland Vegetation Types. *Biology and Environment-Proceedings of the Royal Irish Academy,* **94B,** 119-126.
Melis, C., Buset, A., Aarrestad, P.A., Hansenn, O., Meisinesgt, E.L., Andersen, R., Moksnes, A. & Roskaft, E. (2006) Impact of red deer Cervus elaphus grazing on bilberry Vaccinium myrtillus and composition of ground beetle (Coleoptera, Carabidae) assemblage. *Biodiversity and conservation,* **15,** 2049-2059.
Mills, N. (1994) Parasitoid guilds - defining the structure of the parasitoid communities of endopterygote insect hosts. *Environmental Entomology,* **23,** 1066-1083.
Milner, J.M., Alexander, J.S. & Griffin, A.M. (2002) *A Highland Deer Herd and its Habitat.* Red Lion House, London.
Mohr, D., Cohnstaedt, L.W. & Topp, W. (2005) Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. *Soil Biology & Biochemistry,* **37,** 693-700.

Moran, V. & Southwood, T. (1982) The guild composition of arthropod communities in trees. *The Journal of animal ecology,* **51,** 289-306.

Morris, M. & Plant, R. (1983) Responses of grassland invertebrates to management by cutting .5. Changes in Hemiptera following cessation of management. *The Journal of applied ecology,* **20,** 157-177.

Morris, M.G. (2002) *True Weevils 1: Coleoptera: Curculionidae (Raymondionyminae to Smicronychinae).* Royal Entomological Society, London.

Moss, R. (1981) Effects of grazing by mountain hares and red deer on the production and chemical-composition of heather. *The Journal of applied ecology,* **18,** 487-496.

Mysterud, A. (2006) The concept of overgrazing and its role in management of large herbivores. *Wildlife Biology,* **12,** 129-141.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amequita, S. & Favila, M.E. (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation,* **141,** 1461-1474.

Noyes, J.S. (1989a) The Diversity of Hymenoptera in the Tropics with Special Reference to Parasitica in Sulawesi. *Ecological Entomology,* **14,** 197-207.

Noyes, J.S. (1989b) A Study of 5 Methods of Sampling Hymenoptera (Insecta) in a Tropical Rainforest, with Special Reference to the Parasitica. *Journal of Natural History,* **23,** 285-298.

O'Neill, K.M., Olson, B.E., Rolston, M.G., Wallander, R., Larson, D.P. & Seibert, C.E. (2003) Effects of livestock grazing on rangeland grasshopper (Orthoptera : Acrididae) abundance. *Agriculture Ecosystems & Environment,* **97,** 51-64.

Olff, H. & Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution,* **13,** 261-265.

Oliver, I. & Beattie, A. (1996) Designing a cost-effective invertebrate survey: A test of methods for rapid assessment of biodiversity. *Ecological applications,* **6,** 594-607.

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. & Oksanen, L. (2001) Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography,* **24,** 13-24.

Owen, D.F. & Owen, J. (1974) Species-Diversity in Temperate and Tropical Ichneumonidae. *Nature,* **249,** 583-584.

Peng, R.K., Fletcher, C.R. & Sutton, S.L. (1992) The Effect of Microclimate on Flying Dipterans. *International Journal of Biometeorology,* **36,** 69-76.

Perrins, C.M. & Overall, R. (2001) Effect of increasing numbers of deer on bird populations in Wytham Woods, central England. *Forestry,* **74,** 299-309.

Petit, S. & Usher, M.B. (1998) Biodiversity in agricultural landscapes: the ground beetle communities of woody uncultivated habitats. *Biodiversity and Conservation,* **7,** 1549-1561.

Pigott, C.D. (1983) Regeneration of oak-birch woodland following exclusion of sheep. *Journal of ecology,* **71,** 629-646.

Pollock, M.L., Milner, J.M., Waterhouse, A., Holland, J.P. & Legg, C.J. (2005) Impacts of livestock in regenerating upland birch woodlands in Scotland. *Biological Conservation,* **123,** 443-452.

Poyry, J., Lindgren, S., Salminen, J. & Kuussaari, M. (2004) Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications,* **14,** 1656-1670.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. (1980) Interactions Among Three Trophic Levels: Influence of Plants on Interactions Between Insect Herbivores and Natural Enemies. *Annual Review of Ecology and Systematics,* **11,** 41.

Purvis, G. & Curry, J.P. (1981) The Influence of Sward Management on Foliage Arthropod Communities in a Ley Grassland. *Journal of Applied Ecology,* **18,** 711-725.

Putman, R.J. (1996) Ungulates in temperate forest ecosystems; perspectives and recommendatons for future research. *Forest ecology and management,* **88,** 205-214.

Putman, R.J., Edwards, P.J., Mann, J.C.E., How, R.C. & Hill, S.D. (1989) Vegetational and Faunal Changes in an Area of Heavily Grazed Woodland Following Relief of Grazing. *Biological Conservation,* **47,** 13-32.

Putman, R.J. & Moore, N.P. (1998) Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. *Mammal Review,* **28,** 141-163.

Quicke, D., Laurenne, N., Fitton, M. & Broad, G. (2009) A thousand and one wasps: a 28S rDNA and morphological phylogeny of the Ichneumonidae (Insecta: Hymenoptera) with an investigation into alignment parameter space and elision. *Journal of Natural History,* **43,** 1305-1421.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing.* Vienna, Austria.

Rambo, J. & Faeth, S. (1999) Effect of vertebrate grazing on plant and insect community structure. *Conservation Biology,* **13,** 1047-1054.

Ramos, M., Robles, A. & Castro, J. (2006) Efficiency of endozoochorous seed dispersal in six dry-fruited species (Cistaceae): from seed ingestion to early seedling establishment. *Plant Ecology,* **185,** 97-106.

Ribera, I., Foster, G.N., Downie, I.S., McCracken, D.I. & Abernethy, V.J. (1999) A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). *Annales Zoologici Fennici,* **36,** 21-37.

Rodwell, J.S. (1991) *British Plant Communities. Volume 2 Mires and Heaths.* Cambridge University Press, Cambridge.

Root, R.B. (1967) The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher. *Ecological monographs,* **37,** 317-350.

Rosas, C., Engle, D., Shaw, J. & Palmer, M. (2008) Seed dispersal by Bison bison in a tallgrass prairie. *Journal of Vegetation Science,* **19,** 769-778.

Saaksjarvi, I., Ruokolainen, K., Tuomisto, H., Haataja, S., Fine, P. & Cardenas, G. (2006) Comparing composition and diversity of parasitoid wasps and plants in an Amazonian rain-forest mosaic. *Journal of Tropical Ecology,* **22,** 167-176.

Scheffler, P.Y. (2005) Dung beetle (Coleoptera : Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology,* **21,** 9-19.

Schutz, M., Risch, A.C., Leuzinger, E., Krusi, B.O. & Achermann, G. (2003) Impact of herbivory by red deer (Cervus elaphus L.) on patterns and processes in subalpine grasslands in the Swiss National Park. *Forest Ecology and Management,* **181,** 177-188.

Shaw, M. (1974) The reproductive characteristics of oak. *The British Oak: Its History and Natural History. Botanical Society of the British Isles Conference Report no. 14.* (ed M. G. Morris, Perring, F.H. (Eds.)), pp. pp. 162-181. E.W. Classey Faringdon, Berkshire.

Shaw, M.R. (2006) Habitat considerations for parasitic wasps (Hymenoptera). *Journal of Insect Conservation,* **10,** 117.

Shaw, M.R. & Huddleston., T. (1991) *Classification and Biology of Braconid Wasps (Hymenoptera: Braconidae). Handbooks for the Identification of British Insects.* Royal Entomological Society, London.

Shiponeni, N. & Milton, S. (2006) Seed dispersal in the dung of large herbivores: implications for restoration of Renosterveld shrubland old fields. *Biodiversity and conservation,* **15,** 3161-3175.

Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology,* **79,** 2057-2070.

Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist,* **152,** 738-750.

Simberloff, D. & Dayan, T. (1991) The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics,* **22,** 115-143.

Sjodin, N.E., Bengtsson, J. & Ekbom, B. (2008) The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology,* **45,** 763-772.

Skinner, B. (1984) *The colour identification guide to Moths of the British Isles.* Viking, London.

Slade, E.M., Mann, D.J., Villanueva, J.F. & Lewis, O.T. (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology,* **76,** 1094-1104.

Smith, R.J. & Merrick, M.J. (2001) Resource availability and population dynamics of Nicrophorus investigator, an obligate carrion breeder. *Ecological Entomology,* **26,** 173-180.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: The Priciples and Practice of Statistics In Biological Research.* W.H. Freeman and Company, San Francisco.

Sommaggio, D. (1999) Syrphidae: can they be used as environmental bioindicators? *Agriculture Ecosystems & Environment,* **74,** 343-356.

Southwood, T., Wint, G., Kennedy, C. & Greenwood, S. (2005) The composition of the arthropod fauna of the canopies of some species of oak (Quercus). *European journal of entomology,* **102,** 65-72.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1979) Relationships of Plant and Insect Diversities in Succession. *Biological Journal of the Linnean Society,* **12,** 327-348.

Southwood, T.R.E. & Henderson, P. (2000) *Ecological Methods.* Blackwell Science, Oxford.

Speight, M.C.D., Castella, E., Obrdlik, P. & Lavery, T. (1998) Syrph the Net: the database of European Syrphidae (Diptera) on the Internet. Syrph the Net Publications, Dublin.

Sperber, C.F., Nakayama, K., Valverde, M.J. & Neves, F.D. (2004) Tree species richness and density affect parasitoid diversity in cacao agroforestry. *Basic and Applied Ecology,* **5,** 241-251.

Sroka, K. & Finch, O. (2006) Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). *Journal of Insect Conservation,* **10,** 335-350.

Stewart, A.J.A. (2001) The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. *Forestry,* **74,** 259-270.

Strong, D.R., Lawton, J.H. & Southwood, R. (1984) *Insects on Plants: Community patterns and mechanisms.* Blackwell Scientific Publications, Oxford.

Suominen, O. (1999) Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia. *Ecography,* **22,** 651-658.

Suominen, O. (2003) Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. *Ecography,* **26,** 503-513.

Suominen, O., Danell, K. & Bryant, J.P. (1999) Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain. *Ecoscience,* **6,** 505-510.

Suominen, O., Niemela, J., Martikainen, P., Niemela, P. & Kojola, I. (2003) Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. *Ecography,* **26,** 503-513.

Sutherland, W.J. (2006) *Ecological Census Techniques.* Cambridge University Press, Cambridge, UK.

Taboada, A., Kotze, D., Tarrega, R. & Salgado, J. (2006) Traditional forest management: Do carabid beetles respond to human-created vegetation structures in an oak mosaic landscape? *Forest ecology and management,* **237,** 436-449.

Tadey, M. & Farji-Brener, A.G. (2007) Indirect effects of exotic grazers: livestock decreases the nutrient content of refuse dumps of leaf-cutting ants through vegetation impoverishment. *Journal of Applied Ecology,* **44,** 1209-1218.

Tahvanainen, J. (1982) The influence of host plant growth form and phenology on the life strategies of Finnish macrolepidopterous larvae. *Oikos,* **39,** 164.

Telfer M.G., M.W.R., Lambdon P., Pywell R.F. and Sparks T.H. (2000) The carabids of conventional and widened field margins. . *Aspects ofApplied Biology,* **58,** 411-416.

Thompson, D.B.A. (1995) Upland heather moorland in Great Britain - a review of international importance, vegetation change and some objectives for nature conservation. *Biological conservation,* **71,** 163-178.

Thompson, D.B.A., Macdonald, A.J., Marsden, J.H. & Galbraith, C.A. (1995) Upland Heather Moorland in Great-Britain - a Review of International Importance, Vegetation Change and Some Objectives for Nature Conservation. *Biological Conservation,* **71,** 163-178.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science,* **277,** 1300-1302.

Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature,* **379,** 718-720.

Townes, H. (*1972*) *A light-weight malaise trap*. *Entomological News, **83**, 239-247*.

Usher, M.B. (1992) Management and Diversity of Arthropods in Calluna Heathland. *Biodiversity and Conservation,* **1,** 63-79.

Usher, M.B. & Thompson, D.B.A. (1993) Variation in the Upland Heathlands of Great-Britain - Conservation Importance. *Biological Conservation,* **66,** 69-81.

Vanbergen, A., Hails, R., Watt, A. & Jones, T. (2006) Consequences for host-parasitoid interactions of grazing-dependent habitat heterogeneity. *The Journal of animal ecology,* **75,** 789-801.

Vandenberghe, C., Prior, G., Littlewood, N.A., Brooker, R. & Pakeman, R.J. (2009) Influence of livestock grazing on meadow pipit foraging behaviour in upland grassland. *Basic and applied ecology,* **10,** 662-670.

Vera, F.W.M. (2000) *Grazing Ecology and Forest History.* CABI Publishing, Oxon, UK.

Virtanen, R., Edwards, G.R. & Crawley, M.J. (2002) Red deer management and vegetation on the Isle of Rum. *The Journal of applied ecology,* **39,** 572-583.

Voigt, W., Perner, J. & Jones, T. (2007) Using functional groups to investigate community response to environmental changes: two grassland case studies. *Global change biology,* **13,** 1710-1721.

Waring, P., Townsend, M. & Lewington, R. (2003) *Field Guide to the Moths of Great Britain and Ireland.* British Wildlife Publishing, Hampshire, UK.

Welch, D. (1984a) Studies in the Grazing of Heather Moorland in Northeast Scotland .1. Site Descriptions and Patterns of Utilization. *Journal of Applied Ecology,* **21,** 179-195.

Welch, D. (1984b) Studies in the Grazing of Heather Moorland in Northeast Scotland .2. Response of Heather. *Journal of Applied Ecology,* **21,** 197-207.

Welch, D. (1984c) Studies in the Grazing of Heather Moorland in Northeast Scotland .3. Floristics. *Journal of Applied Ecology,* **21,** 209-225.

Welch, D. (1985) Studies in the Grazing of Heather Moorland in Northeast Scotland .4. Seed Dispersal and Plant Establishment in Dung. *Journal of Applied Ecology,* **22,** 461-472.

Welch, D. (1986) Studies in the Grazing of Heather Moorland in Northeast Scotland V Trends in Nardus-Stricta and Other Unpalatable Graminoids. *Journal of Applied Ecology,* **23,** 1047-1058.

Welch, D. & Scott, D. (1995) Studies in the Grazing of Heather Moorland in Northeast Scotland .6. 20-Year Trends in Botanical Composition. *Journal of Applied Ecology,* **32,** 596-611.

Wilson, J. (1999) Guilds, functional types and ecological groups. *Oikos,* **86,** 507-522.

Woodcock, B.A. (2004) Pitfall trapping in ecological studies. *Insect sampling in forest ecosystems, Methods in Ecology Series.* (ed S. R. Leather). Blackwell Science LTD, Oxford.

Woodcock, B.A., Potts, S.G., Pilgrim, E., Ramsay, A.J., Tscheulin, T., Parkinson, A., Smith, R.E.N., Gundrey, A.L., Brown, V.K. & Tallowin, J.R. (2007a) The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. *Journal of Applied Ecology,* **44,** 60-69.

Woodcock, B.A., Potts, S.G., Westbury, D.B., Ramsay, A.J., Lambert, M., Harris, S.J. & Brown, V.K. (2007b) The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages. *Ecological Entomology,* **32,** 302-311.