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Biodiversity change in the Irish uplands – the effects of grazing management

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This thesis is presented to the National University of Ireland, Cork,
in candidature for the degree of Doctor of Philosophy

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April 2013

Declaration

I hereby declare that the work presented in this PhD thesis is my own work and has not been previously submitted for another degree at any other university or institution.

Roslyn M. Anderson

For my parents, Alan and Fiona Anderson

'What kind of growth will we find underfoot if upland farming declines even further, if sheep numbers collapse and all burning of furze and heather ceases?'

Dermot Somers, The Mountains of Iveragh: A Personal Journey, *The Iveragh Peninsula A Cultural Atlas of the Ring of Kerry*, 2009

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Abstract

The Irish uplands comprise a wealth of semi-natural habitats, including the internationally important blanket bog, protected under the EU Habitats Directive - home to the ground beetle, *Carabus clatratus*. As one of the prominent forms of land use across much of upland Europe, extensive livestock grazing may hold the key to the sustainable management of these landscapes for the benefit of many taxa, particularly as open habitats are vital to many species of conservation concern. However, recent agricultural policy reform has resulted in a decline in sheep numbers in the uplands, leading to concern that the biodiversity value of these areas is under threat. This study quantifies the effects of varying levels of grazing management on plant, ground beetle and breeding bird diversity in both the uplands and lowlands of hill sheep farms in County Kerry, Ireland. The influence of environmental factors such as altitude and soil characteristics is also investigated. Farms represent a grazing continuum of lightly to heavily grazed states, measured using a series of field indicators. Linear mixed effects modelling and the ordination technique, non-metric multidimensional scaling (NMS) are employed as a means of disentangling the management and environmental factors most influential in explaining plant, ground beetle and bird diversity and community composition. A clear altitudinal gradient is evident in the diversity of all three taxa. The majority of species inhabit the lowlands, with the exception of some upland specialists, such as the ground beetle, *Notiophilus aesthuans*. Densities of meadow pipit and skylark are also greater in the uplands. Grazing state may be determined by plant composition, for example, the proportion of *Molinia caerulea* or *Nardus stricta* present, as well as the percentage of traditional ewes on a farm or structural features, such as the percentage of vegetation litter or the percentage of scrub. Soil moisture or soil pH are also important, particularly for plants and ground beetles. Differences in the size and mobility of species will define the most appropriate scale at which to sample. Birds, for example, are influenced at the regional scale, while soil and fine-scale vegetation structure play a more extensive role in plant and ground beetle diversity and distribution. The mode of feeding can determine the categorisation of functional groups, which are, again, affected to varying degrees by grazing and environmental factors. Measures of ecosystem functioning, for example, plant biomass (nutrient cycling and productivity) and the percentage of vegetation cover (erosion rates), are influenced by plant diversity, which is, in turn, influenced by grazing management. Levels of the ecosystem service, soil organic carbon, vary with ground beetle abundance and species richness, potentially influencing carbon sequestration and thereby climate change. The challenge is to manage these high nature value landscapes using agri-environment schemes which enhance biodiversity by maintaining structural heterogeneity across a range of scales, altitudes and habitats, whilst also integrating the decisions of people living and working in these marginal areas.

Chapter 1

General Introduction

‘Mountains enlarge the landscape of the mind’ (Magnus Magnusson, 2005).

The Bridia Valley, County Kerry (Photo: Roz Anderson).

1.1 Background

Mountains comprise nearly a quarter of the world's land surface area and are home to twelve percent of the global population (Price and Hofer, 2005), with a further fourteen percent living adjacent to mountain areas (Meybeck *et al*., 2001). Ecosystem processes and their management on mountain slopes can have direct impacts on the availability and quality of ecosystem goods and services delivered in the lowlands (Edwards, 2005). Mountains provide water, food, fibre, cultural and recreational opportunities. They also shape the climate across broad regions, helping to control erosion, building soils and providing habitats for many species of special interest (Edwards, 2005). Upland ecosystems are globally the source for over fifty percent of all rivers (Bonn *et al*., 2009).

Altitudinal zonation in mainland Europe is generally defined by the climatic effects, such as temperature, on mountain vegetation, the presence of a natural treeline, or the ruggedness or steepness of the terrain (Poore and McVean, 1957; Horsfield and Thompson, 1996; Körner *et al*., 2011; Pecher *et al*., 2011; Thompson *et al*., 2012). No statutory definition of the uplands exists. However the use of the term 'upland' by Ratcliffe (1977) and Ratcliffe and Thompson (1988), referring to those areas lying 'typically above the limits of enclosed farmland' and at altitudes above 200m (Thompson *et al*., 1995; Milne, 1996) are very similar to the definition of mountains by the European Commission Council Regulation 1257/99 (Article 18). Others define the uplands as land within 'Less Favoured Areas' which includes lower hill country, enclosed hill farmland and mountains (House of Commons - EFRACOM, 2011). Habitat or environment has also been used to define the uplands, highlighting, for example, those areas composed of predominantly dwarf shrub heaths, grasslands and peat bogs (Pearsall, 1950; Ratcliffe and Thompson, 1988; Averis *et al*., 2004). It is estimated that about twenty-five percent of Ireland and about thirty percent of Britain is upland (Ratcliffe and Thompson, 1988; Ratcliffe, 1990). Upland environments are unique in nature being both physically and economically remote, as well as presenting extreme climatic conditions. The uplands of Ireland and Britain have particular international significance owing to their unique hyper-oceanic climates (Ratcliffe and Thompson, 1988). Upland environments tend to be wet, windy and cool (Ratcliffe and Thompson, 1988) and soils are predominantly acidic and nutrient poor, as a result of leaching on slopes (Averis *et al*., 2004). This thesis focuses on upland habitats in southwest Ireland, although lowland habitats, primarily improved agricultural grassland, are also examined. These areas are dominated by hill sheep farming and due to recent changes in the Common Agricultural Policy, are facing the threat of undergrazing and in some cases, abandonment.

1.2 Grazing

Agriculture dominates land use over much of the earth, although the majority of this is arable, with grazing lands making up around a third of total agricultural land use (Haberl *et al*., 2007). Farmland now constitutes around forty-five percent of the total land area of Europe (Food and Agriculture Organization of the United Nations, 2011) and therefore plays a major role in shaping the European landscape. Four-fifths of land in Ireland is under agricultural use, with grassland comprising 75.5% of this. In fact, in 1990, Ireland had the largest percentage of permanent pasture of any other EU member state (Cabot, 1999).

In many parts of Europe centuries of deforestation and subsequent extensive pastoralism has led to the creation of semi-natural habitats which support a wide range of species (Kleijn *et al*., 2006). The term 'semi-natural' acknowledges the important role of human activity in the creation of contemporary upland landscapes (Evans, 2009). Grazing by sheep (*Ovis aries*), cattle (*Bos taurus*), goats (*Capra hircus*) and native deer have helped to maintain these open areas (Ratcliffe and Thompson, 1988; Usher and Gardner, 1988; Ratcliffe, 1990; Averis *et al*., 2004). In the mid twentieth century agricultural intensification began to replace more traditional mixed farming systems. The introduction of headage-based subsidies through the Common Agricultural Policy (CAP) saw a substantial growth in sheep numbers in both the uplands and lowlands, along with a corresponding decrease in cattle numbers in the uplands (Robson, 1997; Fuller and Gough, 1999; Dennis, 2003). This intensification led to many areas becoming severely overgrazed resulting in large reductions in farmland biodiversity (Bleasdale, 1998; Midmore *et al*., 1998; Caraveli, 2000; Marriott *et al*., 2009). In 2005 the Single Payment Scheme (SPS) saw the decoupling of subsidies from production, in the form of environment and rural development support (Gardner *et al*., 2009). However, this reduced the incentive to maintain high stocking rates (O'Rourke, 2009) and the removal of sheep from the hills resulted in a rise in undergrazing and land abandonment in many areas (Caraveli, 2000; MacDonald *et al*., 2000; Matthews *et al*., 2006; Acs *et al*., 2010).

Overgrazing and undergrazing are the dominant land pressures reported in an assessment of habitats in Ireland, as part of the EU Habitats Directive (O'Keeffe *et al*., 2008). Overgrazing is difficult to define and has led to particular debate (Midmore *et al*., 1998). Overgrazed land often becomes too degraded for further grazing, allowing competitive, coarse unpalatable grasses such as *Nardus stricta* to predominate at the expense of the more nutritious *Agrostis* and *Festuca* species. Excessive trampling will lead to extended areas of heavily poached ground, which, along with factors such as high rainfall and a reduction in bryophyte cover (Grant and Maxwell, 1988), will lead to soil erosion (Miles, 1988; Sydes and Miller, 1988; Thompson *et al*., 1995; Acs *et al*., 2010; Buckingham *et al*., 2006; Stoate *et al*., 2001). In fact, trampling has been shown to be a far greater problem than grazing or browsing in many areas (Brendan O'Hanrahan, pers. comm.; Oom *et al*., 2008).

Fig. 1.1 Undergrazed site showing bracken (*Pteridium aquilinum*) impeding livestock movement (Photo: Roz Anderson).

In contrast, undergrazing or the 'under-utilisation' of land becomes evident when scrub or coarse vegetation reaches environmentally detrimental levels, with scrub encroachment and the dominance of a few grazing intolerant, but competitive, plant species such as *Molinia caerulea*, *Juncus spp*. and woody dwarf ericoid shrubs (Marriott *et al*., 2004; Caraveli, 2000; Marriott *et al*., 2009) through competitive exclusion (Grime, 1979; Huston, 1979; Tilman, 1982). A reduction in forb species and an increase in dead plant material or rank vegetation results in a shift in species composition to those plant species less easily digested (Marriott *et al*., 2005; Fondell and Ball, 2004). This can lead to an overall reduction in the productivity and diversity of important plant and animal groups (MacDonald *et al*., 2000; Hellegers, 1998;

Marriott *et al.*, 2004; Caraveli, 2000), and may also act as an impediment to livestock movement (**Fig. 1.1**). This polarisation of agricultural practices, intensification in the lowlands and abandonment in the uplands, is likely to threaten the biodiversity of these semi-natural habitats (Stoate *et al.*, 2009). High nature value (HNV) upland habitats are managed through extensive grazing in Europe (Cole *et al.*, 2010), which help to promote habitat heterogeneity, through the effects of selective grazing, trampling and defecating.

The use of stocking rates is by far the most popular method of measuring grazing pressure (Hester *et al.*, 1996; Bertiller *et al.*, 2002; Cole *et al.*, 2006; Austrheim *et al.*, 2008). However, Fuller (1996) has noted that the average stocking density of livestock actually provides no indication of the impact that the animals have on the vegetation and suggest that a habitat-specific stocking rate would be more applicable. Traditional breeds, whose characteristics are often best suited to local conditions (Wright *et al.*, 2002), have been found to graze in a less selective manner than commercial breeds (Dumont *et al.*, 2007) and may therefore hold the key. However, factors such as shepherding, supplementary feeding, time of year and carrying capacity of the landscape (Ratcliffe, 1990; Welch, 1998, Midmore *et al.*, 1998; Dunford and Feehan, 2001) are also crucial.

1.3 Vegetation

Throughout Europe, the intensification or abandonment of traditional farming practices has resulted in the loss of priority habitats for conservation, such as heather moorland or semi-natural grassland (Bignal and McCracken, 1996; 2000). Much of the upland vegetation of Ireland and Britain is distinctly western and oceanic in character and distribution, with some vegetation types such as the blanket bogs (**Fig. 1.2**), wet heaths, *Calluna* heaths and *Racomitrium* moss-heaths being more common in the uplands of Ireland and Britain than anywhere else in Europe (Thompson and Brown, 1992; Averis *et al.*, 2004). Several upland habitats, such as peatland, are protected under the EU Habitats Directive (92/43/EEC) (Crowley *et al.*, 2003), which includes the designation of Special Areas of Conservation (SACs) (**Fig. 1.3**). In fact, it has been estimated that fourteen percent of the habitats listed in the Habitats Directive may actually be threatened by agricultural abandonment (Bignal and McCracken, 1996; Ostermann, 1998). Over seventeen percent of Ireland's land area is peatland, the third largest in Europe. Undamaged, this is one of the few remaining pristine ecosystems in the world, as well as a valuable carbon store (Gorham, 1991; Clymo *et al.*, 1998; Bracken *et al.*, 2008; Connolly and Holden, 2009; CORINE 2006-EPA/EEA, 2009; Connolly *et al.*, 2011).

Fig. 1.2 Blanket bog (Photo: Roz Anderson).

Intensive grazing of bog or peatland may result in a transition to grassland (Miles, 1988; Thompson *et al.*, 1995), while previously wooded regions may become dominated by large areas of bracken (Ratcliffe and Thompson, 1988). Undergrazing is thought to decrease habitat heterogeneity leading to a reduction in biodiversity (Farina, 1997; Benton *et al.*, 2003). Changes in plant species composition may take many years to occur, whereas changes in sward structure, such as height, are often observed within a growing season (Hulme *et al.*, 1999; Critchley *et al.*, 2003; Marriott *et al.*, 2004). Extensive grazing management is thought to enhance the structural heterogeneity of vegetation, increasing plant diversity and providing a mosaic of habitats capable of supporting a variety of species, many of which play a vital role in upland food webs (Grime, 1973, 1979; Milchunas *et al.*, 1988; Puerto *et al.*, 1990). Chapter 2 investigates how plant diversity and species composition are affected by different grazing management regimes across a range of altitudes (upland and lowland habitats) and the impact this has on ecosystem functioning.

1.4 Ground beetles

Arthropod species comprise the majority of taxa in the uplands and are critical in upland food chains (Dennis, 2003). The effects of grazing management on arthropods vary but the majority of studies indicate that the abundance and diversity of arthropods increase under low levels of grazing intensity (Dennis *et al*., 1998; 2001; 2004; 2008; Pöyry *et al*., 2006). Conversely there is also evidence to suggest that lack of grazing can be detrimental to arthropods (González-Megías *et al.*, 2004; Debano, 2006). However, very few studies have looked at the terrestrial, ground-dwelling invertebrates of Irish mountains (McCormack *et al*., 2006; 2009) and so data gathered here will further our understanding of these species, which may be of particular importance in the future, as climate change continues to limit the distributions of many montane species.

Ground beetles (Coleoptera: Carabidae) are one of the most common families of surface-active arthropods in agricultural ecosystems (Cole *et al*., 2002). They are a well-studied family and are sensitive to habitat heterogeneity and land use (Thiele, 1977; Eyre and Rushton, 1989; Blake *et al*., 1996; Lövei and Sunderland, 1996; Niemelä, 1996; Dennis *et al*., 1997; 2002; Ribera *et al*., 2001; Brose, 2003). Functional groups, such as generalist or specialist predators or phytophages are influenced in different ways by management and environmental factors (Lövei, 2008). Size and mobility are also important. Large carabids of the *Carabus* genus are adversely affected by intensive management practices (Luff and Rushton, 1989; Rushton *et al*., 1989; Blake, 1996; Ribera *et al*., 2001; Cole *et al*., 2002, 2005), while specialist carabid predators, such as *Notiophilus* spp., which specialise on Collembola, hunt using visual cues and therefore prefer a more open sward (Cole *et al*., 2006). Changes in the ecological composition of carabid assemblages may have knock-on effects for ecosystem functioning, such as the provision of prey for many declining upland bird species (Dennis, 2003; Cole *et al*., 2002; Buchanan *et al*., 2006). Chapter 3 examines the effects of grazing and altitude (uplands and lowlands) on ground beetle abundance and species composition and considers how this may influence ecosystem functioning or ecosystem services such as carbon sequestration.

1.5 Birds

Agricultural areas are home to more than half of all European bird species and fifty percent of these are either threatened or internationally important. The rise in agricultural intensification in lowland systems has led to a dramatic decline in farmland bird populations (Donald *et al*., 2001; 2006; Nikolov, 2010), yet, few studies have focused on the effects of grazing intensity on upland bird populations (Anderson and Yalden, 1981; Thompson *et al*., 1988; Fuller and Gough, 1999; Critchley *et al*., 2004; Marriott *et al*., 2004; Pollock *et al*., 2005).

The uplands contain many unique breeding bird species including golden plover (*Pluvialis apricaria*), ring ouzel (*Turdus torquatus*), red grouse (*Lagopus lagopus scotica*) and raven (*Corvus corax*), all of which were observed on farms in the present study. They also support high densities of meadow pipit (*Anthus pratensis*) and skylark (*Alauda arvensis*) and provide locally important breeding habitat for wren (*Troglodytes troglodytes*) (Crowe *et al*., 2010; Crowe, 2011; Copland *et al*., 2012). In fact twenty percent of the bird assemblage associated with upland heather moorland in the UK is listed under Annex 1 of the EC Directive on the Conservation of Wild Birds, 79/409/EEC (Thompson *et al*., 1995). Pastoral habitats are known to have suffered more local bird extinctions than arable areas (Atkinson *et al*., 2004).

Overgrazing, particularly by sheep, deteriorates the sward for nesting, altering predation pressure and modifying food supply, such as seed resources or invertebrate prey (Fuller and Gough, 1999; Vickery *et al*., 2001). Although the large-scale regeneration of scrub and woodland can maximise bird diversity (Fuller *et al*., 1999; Gillings *et al*., 2000), it is generally detrimental to open habitat bird species (Coppedge *et al*., 2001; Laiolo *et al*., 2004), favouring more common and widespread species (Stoate *et al*., 2001; Garcia *et al*., 2008). An adequate level of grazing will help to create an open, patchy sward, while the deposition of dung can provide localised sources of invertebrate prey (Tucker, 1992; Wilson *et al*., 1996; Atkinson *et al*., 2005), as well as undigested grains for granivores (Yuan, 1996). Chapter 4 explores breeding bird diversity in the uplands and lowlands and the effects of grazing management and habitat on their alpha, beta and gamma diversity. Chapter 5 investigates the impact of grazing state, altitude and other environmental factors on breeding bird assemblages.

1.6 Spatial scale and ecosystem services

Traditionally, mountain environments were thought to support only ‘simple’ ecosystems, due to the decrease in species richness with altitude. However, the high degree of spatial complexity of mountain landscapes suggests that their ecosystems should actually be highly complicated (Haslett, 1997).

Few studies have examined the interactive relationship between scale and pattern-driving processes such as grazing (Fuhlendorf and Smeins, 1999). However, the effects of grazing on plant and animal species are thought to vary according to the scale of observation because large herbivores do not graze in a uniform manner (Clarke *et al*., 1995; Hester *et al*., 1999) and different taxa perceive and respond to their environment at different spatial scales (Addicott *et al*., 1987; Wiens, 1989; Wiens *et al*., 1997; Cushman and McGarigal, 2002; Olff and Ritchie, 2002; Tscharntke and Brandl, 2004; Bossenbroek *et al*., 2005; González-Megías *et al*., 2007). Small organisms generally respond to their environment at a small scale (Barton *et al*., 2009); however, it should not be assumed that small organisms, such as beetles, only respond to their environment at the fine scale or that larger and more mobile species, such as birds, respond to variables only at a broad scale (Bossenbroek *et al*., 2005). Many species and assemblages respond at multiple scales as they require multiple resources over their life cycles or have large home ranges (Gabriel *et al*., 2010).

There is growing concern that a decline in biodiversity may adversely impact the functioning of agricultural ecosystems and therefore the sustainability of associated ecosystem services (Flynn *et al*. 2009; Cole *et al*., 2012). Plant functional traits may influence primary productivity, standing biomass, and litter decomposition, which can directly influence ecosystem services (Díaz *et al*., 2007; Lavorel *et al*., 2011; Ford *et al*., 2012; Lienin and Kleyer, 2012). Ground beetles may act as pest control agents (Lövei and Sunderland, 1996; Mair and Port, 2001; Peterson *et al*., 2004) or as food for farmland birds (Poulsen *et al*., 1998). Birds provide a cultural, revenue generating service through bird watching (Whelan *et al*., 2008) and may link ecosystem processes separated by great distances through flight (Whelan *et al*., 2008). They also, like ground beetles, can act as pest control agents of invertebrate and weed species, or as scavengers, seed dispersers or ecosystem engineers (Sekercioglu, 2006; Kellermann *et al*., 2008). Chapter 6 examines the relationship between spatial scale and grazing across altitudinal ranges for all three taxa (plants, ground beetles and birds) and determines the scale or multiple scales at which they respond and investigates which species may be driving these responses.

1.7 Management implications

Agri-environment schemes are a means of compensating farmers for any loss of income associated with biodiversity-enhancing land use changes (Kleijn and Sutherland, 2003), particularly in marginal farming areas such as the uplands where the major land uses are based on grazing (Díaz *et al*., 2007). However, there is strong debate over whether or not these schemes are effective in enhancing ecological diversity (Kleijn *et al*., 2001; Peach *et al*., 2001; Kleijn and Sutherland, 2003; Bradbury *et al*., 2004; Vickery *et al*., 2004; Rath *et al*., 2005; Tscharntke *et al*., 2005; Kleijn *et al*., 2006).

Grazing is the most geographically expansive land use in the world, occurring on over a third of the earth's surface (Liu *et al*., 2012), and therefore has the potential to sequester a large proportion of greenhouse gases as carbon in the soil, thereby helping to mitigate climate change (Scurlock and Hall, 1998). Ireland's blanket bogs are not only a substantial store for carbon, but also a large potential sink of atmospheric carbon (Worrall and Evans, 2009; Szyszko *et al*., 2011). It is now thought that only 21% of Ireland's blanket bogs remain in a relatively intact condition (O'Connell, 2001), 54,220 ha of this have been seriously degraded by overgrazing (Cabot, 1999). The uplands have been identified as being particularly vulnerable with respect to climate change (IPCC, 2007). Climate change influences the migration of plant species upwards on mountain peaks (Pauli *et al*., 2003) and an increasingly warm and wet climate may encourage the spread of graminoids and bryophytes at the expense of dwarf-herb vegetation (Geddes and Miller, 2012). Beetles are predicted to respond to climate change by dispersal (Ashworth *et al*., 2001) and sward height has been shown to alter thermal conditions at rates above those predicted by climate change (Suggitt *et al*., 2011). However, Gillingham *et al*. (2012) revealed that, following a 4°C rise in temperature, the landscape was found to be completely unsuitable for the ground beetle, *Carabus glabratus*. Upland birds are thought to be particularly vulnerable to climate change (Pearce-Higgins *et al*., 2009), which may lead to a phenological mismatch, as birds fail to breed at the time of maximal food abundance (Moss *et al*., 2005; Both *et al*., 2006).

The aim of this research is to enhance the understanding of how changes in grazing management can interact with environmental factors in the uplands of the Iveragh Peninsula influencing plant, ground beetle and bird diversity. This will provide an indication of the health and functioning of these ecosystems and help to determine potential benefits to ecosystem services. It is hoped that findings may be implemented in future agri-environment schemes for the area and also considered for hill sheep farms further afield. The main objectives of the study are to: (i) test whether grazing management, altitude and other environmental factors have an effect on plant species diversity, species composition and plant functional diversity and if drivers of ecosystem services are, in turn, affected by grazing management, environmental factors and plant diversity. (ii) to investigate how ground beetles are influenced by grazing management, altitude and factors such as soil moisture and to determine the extent to which carabid abundance, species richness and consumption affect soil organic carbon content and therefore the ecosystem service of carbon sequestration. (iii) to assess the impacts of grazing state, altitude and habitat on upland breeding bird alpha, beta and gamma diversity and to investigate how the bird assemblages of hill sheep farms are influenced by both management and environmental factors. (iv) to examine the significance of spatial scale for plant, ground beetle and bird assemblages across grazing state and altitudinal categories and to determine which species are important in explaining compositional similarity or dissimilarity.

1.8 Study overview

This study was part of the BioUp (Biodiversity Change in the Irish Uplands) Project, which aimed to gain a better understanding of the ecological, social and economic challenges facing the uplands of the Iveragh Peninsula (51° 94′ N, 9° 89′ W) in County Kerry, southwest Ireland (**Fig. 1.3**). Translation of the research for stakeholders was an important element of the project and details are provided in **Appendix B** – 'Farming the Iveragh uplands: A tale of humans and nature'. As a mountainous region of Ireland, dominated by hill sheep farming, it was considered an ideal model for the investigation of upland grazing on biodiversity. Blanket bogs, heaths and acid grasslands typify the area (**Fig. 1.4**), which is home to many plant and animal species of international significance. Seven geographically distinct study areas were selected as being representative of upland grazing conditions across the peninsula. Within each of these areas, three hill farms of varying levels of grazing intensity were identified and a total of twenty-one farms surveyed for different elements of the project (**Table 1.1** & **Fig. 1.5**). Grazing impacts were quantified using a series of field indicators such as sward height, plant litter, bare ground or presence of dung (MacDonald *et al.*, 1998).

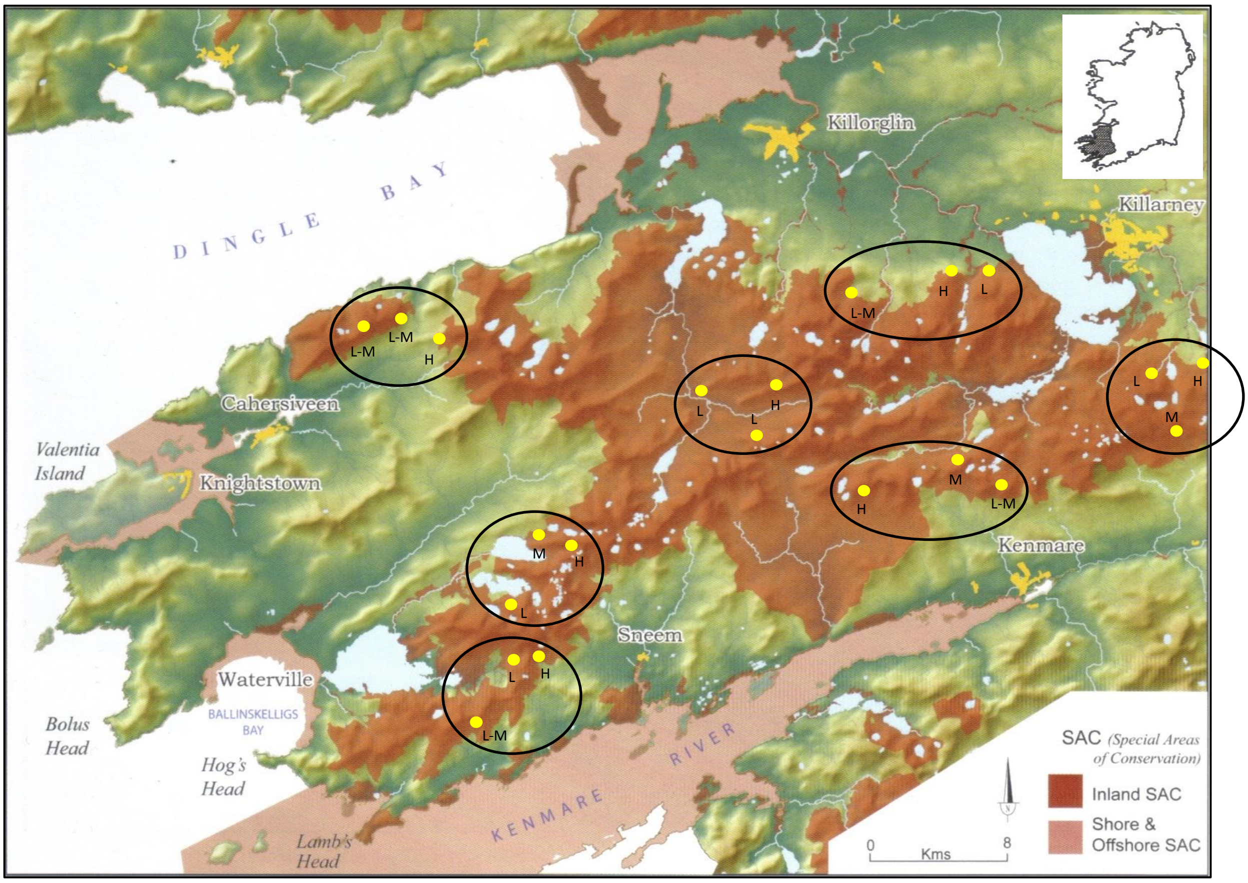

Fig. 1.3 Small map of Ireland highlighting County Kerry. The Iveragh Peninsula is the broad peninsula in the middle of the county. Large map shows Special Areas of Conservation (SACs) (Source: National Parks and Wildlife Service). Yellow dots mark positions of twenty one study farms, separated into 7 areas. L = lightly, L-M = lightly-moderately, M = moderately, H = heavily grazed.

Grazing, as the dominant land use across much of upland Europe, has the potential to help maintain and increase levels of biodiversity and ecosystem functioning in the uplands. The following chapters will investigate this. Chapter 2 discusses the impact of grazing management and environmental factors such as altitude or soil characteristics on plant species diversity, functional diversity and composition. Of key interest is whether the percentage of traditional ewes in a flock interacts with altitude to affect plant species richness. Measures of ecosystem functioning (biomass and total percentage cover) are also predicted to be influenced by plant functional group and species richness. The influence of grazing management, altitude and soil factors on carabid abundance, species richness and assemblage (as well as on staphylinid and other beetle abundance) is investigated in Chapter 3. It also aims to determine the extent to which the ecosystem service of carbon sequestration is affected by carabid abundance and consumption rate.

Table 1.1 All study farms, numbers in italics indicate highest and lowest farm elevations and largest and smallest farm areas.

Area	grazing state	maximum farm altitude (m)	farm area (ha)
Beaufort	L	735	153
Beaufort	L-M	***1010***	69
Beaufort	H	781	55
Bridia Valley	L	***220***	***20***
Bridia Valley	L	663	150
Bridia Valley	H	784	162
Kells	L-M	608	44
Kells	L-M	633	44
Kells	H	550	80
Sneem	L	650	400
Sneem	L-M	470	81
Sneem	H	590	87
Dromid	L	628	364
Dromid	M	400	239
Dromid	H	553	248
Moll's Gap	L-M	492	***1214***
Moll's Gap	M	541	105
Moll's Gap	H	595	162
Mucross	L	782	81
Mucross	M	843	194
Mucross	H	408	79

Chapter 4 examines the impact of varying levels of grazing on upland bird species density and measures of alpha diversity (Simpson's diversity, species richness and evenness), beta and gamma diversity. Effects of altitude, habitat type and vegetation structure are also considered. Chapter 5 investigates how bird assemblages differ from lightly to heavily grazed sites and across altitudinal gradients. Influential habitat and vegetation factors are also discussed and functional groups (insectivores, granivores, omnivores, scavengers) and individual species investigated with respect to grazing, altitude and habitat. The effects of grazing state and altitude on the variation in community composition between plants, ground beetles and birds across three spatial scales is established in Chapter 6. Indicator species are highlighted, which determine similarity within and dissimilarity between grazing states and altitudes. Finally, Chapter 7 considers the findings of previous chapters and evaluates them with regard to past and current research in the field. Implications for management and potential areas of future research are then discussed.

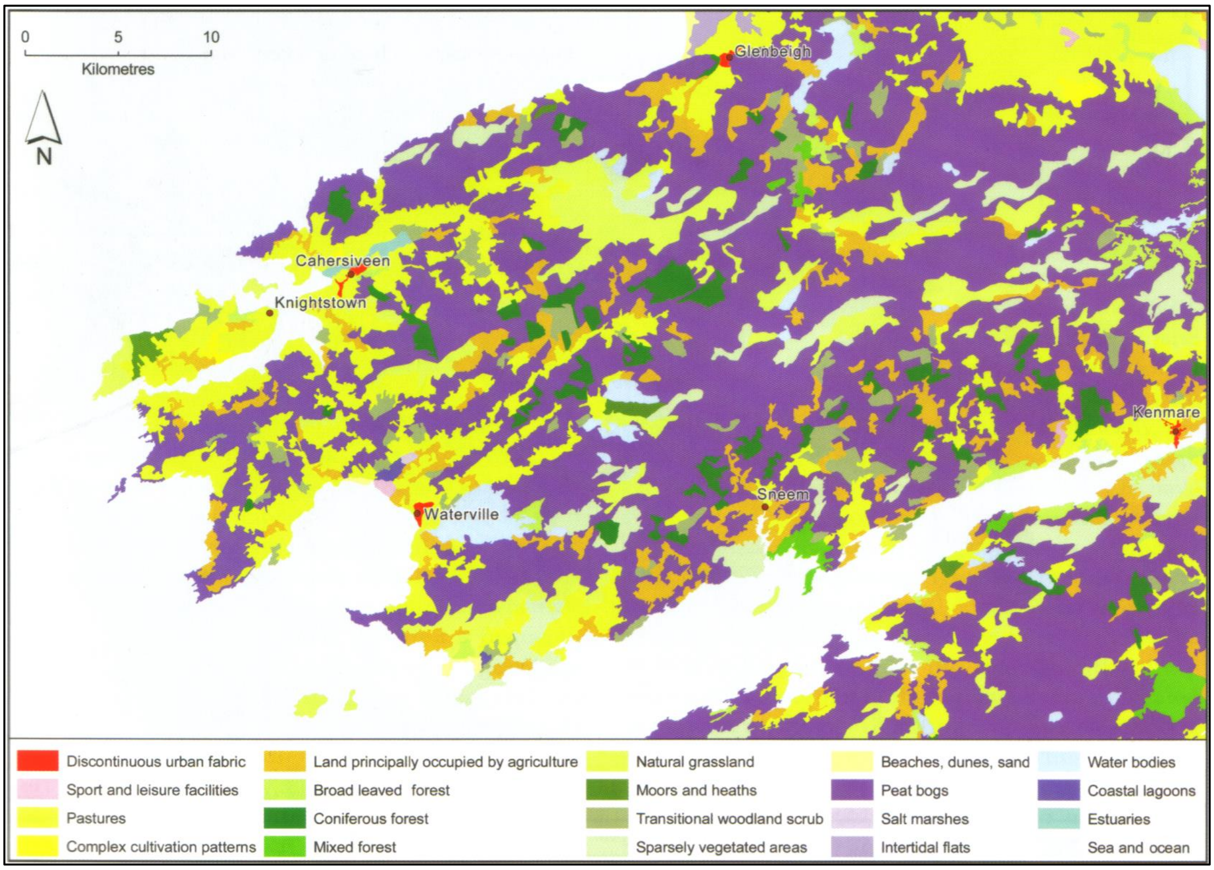

Fig. 1.4 Corine land cover map of the Iveragh Peninsula, derived from satellite imagery. Notice the large coverage of peat bog. (Source: EPA Ireland and European Environment Agency).

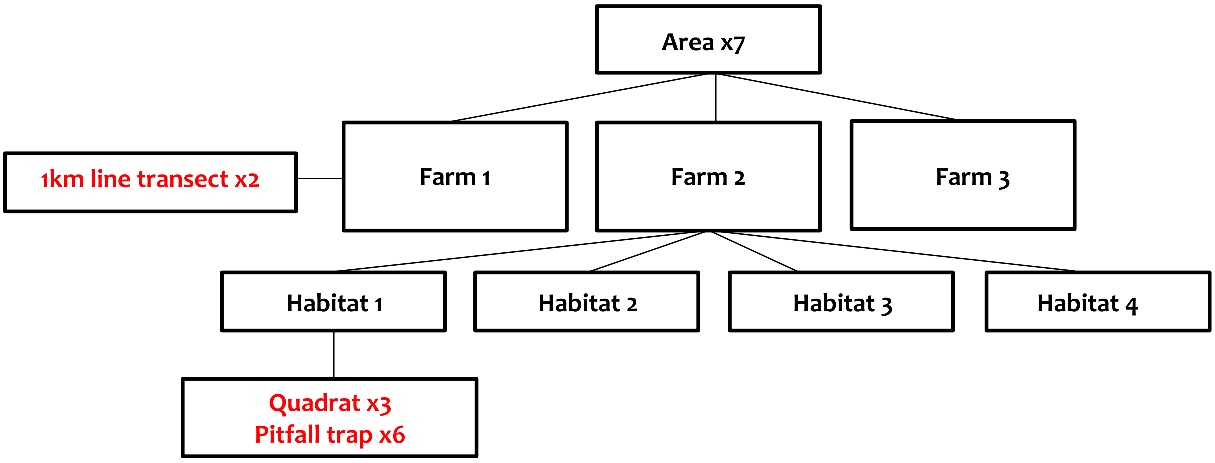

Fig. 1.5 Design of study, showing that plants and beetles were sampled per habitat using quadrats and pitfall traps, respectively, and birds were sampled per farm (two 1km line transects).

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Chapter 2

Characterisation of upland vegetation under varying levels of grazing management: Effects on plant diversity, composition and drivers of ecosystem services

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Heath milkwort (*Polygala serpyllifolia*) (Photo: Roz Anderson).

2.1 Abstract

Upland farming in Europe traditionally involved extensive pasture grazing, which lead to the creation of semi-natural habitats and the provision of food for a wide variety of species. Over the last few decades changes in the Common Agricultural Policy have resulted in the polarisation of hill farming, generally resulting in heavier grazing in the lowlands and a corresponding reduction in upland grazing. Very little is known about the effects of grazing management on the diversity of upland flora in Ireland. This study investigated the impacts of environmental and management factors on plant species diversity and plant functional diversity using classification techniques (TWINSPAN), ordination (Non-metric multidimensional scaling (NMS)) and linear modelling (LMM and GLMM). Vegetation was sampled from 12 farms in County Kerry in the southwest of Ireland in 2007. Classification highlighted clear groupings, which reflected habitats and plant communities, as well as possible management regimes. Ordination demonstrated that soil characteristics and grazing management could explain the majority of the variation in plant species composition. The percentage of traditional ewes reflected traditional management at the farm scale, and accounted for variation in plant species richness, with farms containing 50% traditional and 50% commercial ewes exhibiting the lowest plant species richness. The effects of percentage of traditional ewes on plant species richness varied with altitude, indicating that perhaps a flock comprising wholly of traditional or wholly of commercial breeds may provide the greatest opportunity to maintain plant diversity. Altitude had a positive impact on functional group richness and evenness, as well as on plant biomass, which potentially influences the supporting ecosystem services of primary production and nutrient cycling. Functional group richness also exhibited a positive effect on biomass. The altitudinal effect on biomass may be explained by lower decomposition rates in the uplands. There was a positive relationship between plant species richness and total percentage cover, which potentially affects the regulating ecosystem service of erosion control and reflects processes such as resource use (light), productivity, and soil stabilisation. This study has shown that plant species diversity and plant functional diversity are affected by grazing management, as well as environmental factors and these, in turn, influence ecosystem functioning and potentially ecosystem services.

2.2 Introduction

2.2.1 Background

Upland farming in Europe traditionally involved low intensity mixed grazing, enabling the creation of semi-natural habitats hosting a diverse range of species (MacDonald *et al.*, 2000). The advent of headage-based subsidy payments through the Common Agricultural Policy (CAP), however, encouraged high sheep (*Ovis aries*) numbers and overgrazing in many parts of Europe. Agricultural intensification over the second half of the 20th century led to large reductions in farmland biodiversity (Marriott *et al.*, 2009). The recent decoupling of policy from production has led to a decrease in livestock numbers, resulting in undergrazing and land abandonment in many areas (Caraveli, 2000; Matthews *et al.*, 2006; Acs *et al.*, 2010). These changes in land use are often major drivers of biodiversity change (Pakeman and Marriott, 2010) and are considered to be the most important driving force for vegetation change (Tasser and Tappeiner, 2002), influencing ecosystem function and ultimately the provision of ecosystem goods and services, with the exception of regions experiencing high levels of wild herbivore grazing (Quétier *et al.*, 2007; Gross *et al.*, 2008). Biomass and percent cover are known to be good measures of ecosystem functioning and a high percent of cover (> 100%) should be expected when the vegetation structure is complex (Naeem *et al.*, 1995; Tilman *et al.*, 1997; Allen-Diaz and Jackson, 2000; Schwartz *et al.*, 2000). In fact, vegetative cover has been shown to be directly related to erosion rates (Busby *et al.*, 1994), making it an important ecosystem process in grazed upland ecosystems. Percent cover may influence the regulating ecosystem service of erosion control, particularly important in mountains, moorlands and heaths, while plant biomass may influence the supporting ecosystem services of primary production and nutrient cycling (UK National Ecosystem Assessment, 2011). The introduction of agri-environment measures was an instrument used to compensate farmers for any loss of income associated with biodiversity-enhancing land use changes (Kleijn and Sutherland, 2003), particularly in marginal farming areas such as the uplands where the major land uses are based on grazing (Díaz *et al.*, 2007). As well as recognising that intensification had negative consequences for biodiversity, these schemes also adopted measures to avoid land abandonment, equally detrimental in environmental terms (Commission of the European Communities, 2001). This study investigated the effects of grazing management and environmental factors, such as altitude, on plant biodiversity and the potential drivers of associated ecosystem services of upland systems, an area which has largely remained unexplored.

The uplands may be defined as any area above a certain altitude (e.g. 200m) or above the upper limit of enclosed farmland (Thompson *et al*., 1995; Milne, 1996). They may also be characterised by their environment, which tends towards wetter, windier and cooler conditions (Ratcliffe and Thompson, 1988). Upland soils are predominantly acidic, less productive than those of the lowlands and are nutrient poor, as a result of leaching on slopes. Much of the variation in upland landscapes can be explained by physical factors such as rock type, topography, soils and climate (Averis *et al*., 2004). However, it is also these differences which determine the livestock carrying capacity of each upland habitat (Ratcliffe, 1990). Many upland habitats, together with their flora and fauna are of international conservation importance. Several upland habitats, such as blanket bog, are protected under the Habitats Directive, which includes the designation of Special Areas of Conservation (SACs).

2.2.2 Grazing management

Extensive farming systems are seen as sustainable and there is evidence to suggest that a moderate level of grazing will enhance the structural heterogeneity of vegetation, increase plant diversity and provide a mosaic of habitats capable of supporting a variety of species, many of which play a vital role in upland food webs (Grime, 1973, 1979; Milchunas *et al*., 1988; Puerto *et al*., 1990). However, overgrazing and undergrazing were the dominant detrimental land pressures reported in an assessment of habitats in Ireland, as part of the EU Habitats Directive (O'Keeffe *et al*., 2008). Overgrazing is difficult to define and has led to particular debate (Midmore *et al*., 1998). Overgrazed land often becomes too degraded for further grazing, allowing competitive, coarse unpalatable grasses such as *Nardus stricta* to predominate at the expense of the more nutritious *Agrostis* and *Festuca* species. Excessive trampling will lead to extended areas of heavily poached ground, which, along with factors such as high rainfall and a reduction in bryophyte cover (Grant and Maxwell, 1988), will lead to soil erosion (Miles, 1988; Sydes and Miller, 1988; Thompson *et al*., 1995; Acs *et al*., 2010; Buckingham *et al*., 2006; Stoate *et al*., 2001). In fact, trampling has been shown to be a far greater problem than grazing or browsing in many areas (Brendan O'Hanrahan, pers. comm.; Oom *et al*., 2008). In contrast, undergrazing may lead to scrub encroachment and the dominance of a few grazing intolerant, but competitive, plant species such as *Molinia caerulea*, *Juncus spp*. and woody dwarf ericoid shrubs (Marriott *et al*., 2004; Caraveli, 2000; Marriott *et al*., 2009) through competitive exclusion (Grime, 1979; Huston, 1979; Tilman, 1982). A reduction in forb species and an increase in dead plant material or rank vegetation results in a shift in species composition to those plant species less easily digested (Marriott *et al*., 2005; Fondell and Ball, 2004). This can lead to an overall reduction in the productivity and diversity of important plant and animal species as well as functional groups (MacDonald *et al*., 2000; Hellegers, 1998; Marriott *et al*., 2004; Caraveli, 2000), and may also act as an impediment to livestock movement. Consideration of plant functional traits may allow results to be generalised across diverse environments and may prove more influential than individual plant species in explaining ecosystem functioning measures such as productivity or in explaining the response of plants to management factors such as grazing (Pakeman and Marriott, 2010).

2.2.3 Measuring grazing pressure

Quantifying grazing impacts is not a trivial exercise and many methods have been adopted for measuring grazing pressure. The use of stocking rates is by far the most popular approach (Hester *et al*., 1996; Bertiller *et al*., 2002; Cole *et al*., 2006; Austrheim *et al*., 2008). Seasonal stocking rates have also been investigated (Hulme *et al*., 2002; Holland *et al*., 2008), as have stocking rates across varying scales (Fuhlendorf and Smeins, 1999). Although grazing research has generally focused on examining the effects of grazed versus ungrazed areas (Pyke and Marty, 2005), or the influence of time since the cessation of grazing (Pykälä, 2003), comparing the effects of various grazing intensities has often been viewed as more meaningful (Wallis De Vries and Raemakers, 2001). Some studies have found no effects of livestock breed on plant or animal diversity, while the level of grazing intensity has shown clear effects (Scimone *et al*., 2007; Wallis De Vries *et al*., 2007). Traditional breeds, whose characteristics are often best suited to local conditions (Wright *et al*., 2002), do not appear to have a production advantage over commercial breeds on extensively grazed pastures (Isselstein *et al*., 2007), although they have been found to graze in a less selective manner than commercial breeds (Dumont *et al*., 2007). Alternative approaches have quantified the effects of an unknown stocking rate on the vegetation structure by measuring factors such as forage height (Mapfumo *et al*., 2000), the proportion of herbs eaten (Kausrud *et al*., 2006; Evju *et al*., 2006) or the amount of shoots, leaves or flowers grazed (Oom and Hester, 1999;

Brak *et al*., 2004; Pollock *et al*., 2005). Assessing the general damage to the vegetation and ground by grazing animals has also been used (Thompson *et al*., 2004), recording features such as the extent of bare peat or the condition of the heather (Crushell and O'Callaghan, 2008), or the amount of dung, grazing-damaged shrubs or extent of livestock footprints (Anderson and Hoffman, 2007). Some studies have used a set of field indicators, including the accumulation of dead plant material (litter) and the cover of bare ground, along with measures of species composition and frequency cover to evaluate disturbance (MacDonald *et al*., 1998; JNCC, 2008). Pollock *et al*. (2013) have developed a selection of rapidly-measured biodiversity indicators for rangeland environments by eliciting stakeholder and professional opinion. Others have used a simple index of no grazing, light grazing, moderate grazing or heavy grazing (Norris *et al*., 1998). The impact of grazing on the environment is often dependent upon factors such as shepherding, breed of animal, supplementary feeding and time of year (Welch, 1998, Midmore *et al*., 1998; Dunford and Feehan, 2001). In fact the decline in traditional practices, such as shepherding, may result in heavier pressure on some upland areas, with grazing no longer confined to areas of beneficial forage at certain times of the year (MacDonald *et al*., 2000). Fuller (1996) has noted that the average stocking density of livestock actually provides no indication of the impact that the animals have on upland vegetation and suggest that a habitat-specific stocking rate would be more applicable. It is for this reason that the percentage of traditional ewes was examined in this study, as opposed to solely concentrating on average farm stocking rate.

2.2.4 Effects of grazing on vegetation

Plant species composition may reveal much about past or present management (Benton *et al*. 2003; Usher and Gardner, 1988), environmental conditions, soils, habitat and the surrounding vegetation. However, changes in plant species composition may take many years to occur, whereas changes in sward structure, such as height, are often observed within a growing season (Hulme *et al*., 1999; Critchley *et al*., 2003; Marriott *et al*., 2004). The upland vegetation in the present study is dominated by semi-natural grasslands, blanket bog and wet heaths, in contrast to the agriculturally improved pasture of the lowlands. Ireland is one of Europe's last strongholds for blanket bog and although much of the vast coverage (one million ha) remains intact, large areas have been drained for grazing, cut away or afforested, resulting in widespread fragmentation (Cross, 1989). Intensive grazing on bog may result in the transition to grassland (Miles, 1988; Thompson *et al*., 1995).

This study tested the following hypotheses: 1. Grazing management (% traditional ewes) affects plant species diversity and plant functional diversity. 2. Environmental factors (altitude and soil) influence plant species composition and diversity and 3. Potential drivers of ecosystem services (plant biomass and total percentage cover) are affected by grazing management, environmental factors and plant diversity.

2.3 Methods

2.3.1 Study area

The Iveragh Peninsula (51° 94´ N, 9° 89´ W) is situated in County Kerry, southwest Ireland and covers an area approximately 1400km^2. 65 percent of this isolated peninsula may be classified as upland (O'Rourke and Kramm, 2009; Crowley and Sheehan, 2009). The parent rock is old red sandstone (Higgs, 2009) and the majority of soils are nutrient deficient peaty podzols and blanket peats, which, along with an annual rainfall of over 1500mm, give rise to the vast blanket bogs and heaths which characterise the area (Carruthers, 1998; Averis *et al*., 2004; Crowley and Sheehan, 2009). Land use in these marginal areas is limited and is presently dominated by hill sheep farming.

Four geographically distinct study areas within Iveragh were selected as being representative of upland grazing conditions across the peninsula. Within each of these areas, three hill farms of varying grazing management intensity were identified. The area of managed farmland generally extended between altitudes of 400 and 800m, although total farm sizes were normally less than 250ha. Sheep stocking rates ranged from 0.06 – 0.76 LU/ha over the whole farm and 0.005 – 0.48 LU/ha in the uplands. Stocking rates alone were not found to influence plant diversity measures and so were not included in the analysis.

2.3.2 Grazing state classification

Following an initial visit in 2007, all farm habitats were mapped (Fossitt, 2000; Hill *et al*., 2005). Each farm generally consisted of a heterogeneous mosaic of grazing intensities and habitats. The majority of habitats surveyed were improved grassland, lowland blanket bog, upland blanket bog and dry-humid acid grassland. In total, 144 2m x 2m relevés were sampled across twelve farms. Relevés were chosen by selecting a transect as close to the centre of a habitat as possible (and as homogeneous as possible, avoiding unusual features) and placing three quadrats along it, each 10m from the last. The impacts of grazing, browsing and trampling by large herbivores in upland habitats were quantified by adopting the standard methodology of MacDonald *et al*. (1998). A series of directly observable habitat-specific field indicators, including the accumulation of dead plant material (litter), cover of bare ground, selectivity of grazing and presence of dung, were used. For each field indicator light, moderate and heavy (L, M and H, respectively) impact categories were employed to evaluate the alternative states. An overall estimation for a particular habitat type was then derived by assessing each field indicator separately using a number of relevés. In order to account for spatial heterogeneity, a method of summarising the impact across a habitat was devised, using the percentage of the area occupied by each impact class (Agresti, 1984; Brewer *et al*., 2004; Albon *et al*., 2007). This resulted in the smoothing of the three class impact scale into a more continuous five point scale by introducing intermediate classes light/moderate (L/M) and moderate/heavy (M/H), (after Albon *et al*. 2007). Others have adopted a similar system by allocating weightings to each L, M or H indicator in order to arrive at a numerical sum for each surveyed area (O'Hanrahan, 2005).

Table 2.1 Distribution of farms across grazing states.

	Grazing state				
Number of farms	Light	Light-moderate	Moderate	Moderate-heavy	Heavy
	4	4	0	0	4

2.3.3 Management classification

Although all twelve farms had been allocated a particular grazing state, e.g. lightly grazed, lightly-moderately grazed or heavily grazed (see **Table 2.1**), these classifications were attained through detailed analysis of the vegetation; therefore it was decided not to use these classifications in the analysis of plant diversity. Instead, the management variable, percentage of traditional ewes per farm was adopted. This information was gathered as part of a farm management survey, and the data was divided into four categories: category 1 = 0% traditional ewes, category 2 = 50% traditional ewes, category 3 = 70% traditional ewes and category 4 = 100% traditional ewes. For a comparison of percentage of traditional ewes and sheep stocking rates per farm see **Table 2.2**. The traditional sheep breed on the Iveragh Peninsula was the Scottish Blackface ewe. They are extensively farmed to produce store lambs, which are then finished (fattened for re-sale) by lowland farmers (O'Rourke *et al*., 2012). Domesticated sheep are known to have lived in Ireland long before they were reared by monks in the 12th century. These ancient breeds, which gave rise to the Irish mountain breed, were typically brown in colour and had short wool (Scharff, 1922). However crossbreeding has significantly modified these ancient breeds and most breeds of sheep in Ireland today were brought over from Britain and other countries in the last two hundred years (Scharff, 1922). The Scottish Blackface sheep, in particular, had arrived in Ireland by the mid 19th century (Wool and Sheep, 2009), and as such, is one of the most traditional breeds of sheep in Ireland today.

2.3.4 Soil sampling

The average soil depth (cm) was calculated using four measurements per relevé. Ten 10cm soil cores (Bardgett *et al*., 2001) were collected from each habitat per farm, the cores were collected according to a 'W' pattern (Tytherleigh and Peel, 2003; Marriott *et al*., 2005; Usher *et al*., 2006), and then bulked. Soil pH was determined on fresh soil using distilled water in a soil:water ratio of 1:2 (Ball, 1976; Western States Laboratory Proficiency Testing Program, 1996); Mapfumo *et al*., 2000). The remainder of the samples were stored at 1 – 4 °C and subsequently oven dried at 40 °C (Schaffers and Sýkora, 2000). Samples were then ground to pass through a 2mm sieve (Ball, 1976; Mapfumo *et al*., 2000). Total Kjeldhal Nitrogen was determined using the Kjeldhal method (Mapfumo *et al*., 2000; Persson *et al*., 2008). Soil organic matter was measured using the standard loss on ignition method (Western States Laboratory Proficiency Testing Program, 1996; Heiri *et al*., 2001). Extractable soil phosphorus was estimated using Morgan's extracting solution (Western States Laboratory Proficiency Testing Program, 1996) and percentage soil moisture content was determined (Ball, 1976; Rothamsted Research Soil Microbial Biomass Research Group web page, accessed 2009; Snyder *et al*., 2002).

2.3.5 Structural and environmental variables

Vegetation height (cm) was measured using a sward stick at five points within each relevé and an average calculated. The sward stick is the most appropriate method for measuring structural heterogeneity within vegetation (Stewart *et al*., 2001). Altitude (m), slope, aspect, drainage, firmness and percentage cover of exposed rock, litter, bare ground and dung were also recorded for each relevé (Dunne, 2000; Dunford, 2001; Hodd, 2007). After recording plant percentage cover, all vegetation within an area of 0.25 m^2 inside each 2 m x 2 m relevé was clipped to ground level. Samples were sorted into four major plant growth forms:

graminoids, forbs, dwarf shrubs and mosses and oven dried at 80 ° C for 48 hours, then weighed to estimate total above ground biomass (Gordon, 1989; Gardner *et al.*, 1997; Holland, 2000), ranging from 1.45 – 395.24 g.

ArcGIS 9 (2008) was used to digitise habitat maps for each farm, which allowed the calculation of variables such as habitat diversity (Shannon-Wiener index) as well as the estimation of total area of each habitat per farm.

Table 2.2 The range of sheep stocking rates (LU/ha) against % traditional ewe categories.

farm	sheep stocking rate cat	sheep stocking rate LU/ha	% traditional ewes cat	% traditional ewes
1	1	0	1	0
2	1	0.17	1	0
3	1	0.18	4	100
4	1	0.18	4	100
5	1	0.18	3	70
6	2	0.33	4	100
7	2	0.33	4	100
8	3	0.41	1	0
9	3	0.44	4	100
10	3	0.46	4	100
11	4	0.75	2	50
12	4	0.76	2	50

2.3.6 Data analysis

2.3.6.1 Plant diversity, species richness and evenness

The Braun-Blanquet scale was used, for its simplicity, to estimate the percentage cover of plant species: r: extremely rare, +: cover < 1%, 1: cover 1% - 5%, 2: cover 6% - 25%, 3: 26% - 50%, 4: 51% - 75%, 5: 76% - 100% (Magurran, 1988; Kent and Coker, 1992; Lepš and Hadincová, 1992).

Aspects of local scale diversity were assessed using a number of metrics: species richness, diversity and evenness (Pöyry *et al.*, 2004).

Species diversity was calculated using the Shannon-Wiener index (ranging from 0.30 – 2.96):

$$H' = -\sum_{i=1}^{s} P_i \ln P_i$$

Where s is the number of species, P_i is the proportion of individuals found in the *i*th species expressed as a proportion of total cover and ln is log base$_n$

Species richness was calculated as the total number of species in a sample (ranging from 4 – 26; 133 species in total) and evenness was determined by dividing Shannon-Wiener index by the natural log of the maximum value Shannon-Wiener's could take (i.e. total species richness) and ranged from 0.19 – 0.92:

$$\mathrm{E}H' = H' / \ln(H'_{\mathrm{max}})$$

In order to calculate plant species diversity, the Braun-Blanquet scale values were transformed to percentage cover values using the midpoint of each percentage range, i.e. r, +, 1, 2, 3, 4, and 5 were converted to values of 0.1%, 1.0%, 2.5%, 15.0%, 37.5%, 62.5% and 87.5%, respectively (van der Maarel, 1979; Pyšek *et al.*, 2004). However these values were only used in the univariate analysis. Original Braun-Blanquet values were used in the multivariate analysis (Podani, 2006).

2.3.6.2 Plant functional group diversity, richness and evenness

Nine functional groups were determined: grasses, forbs, mosses, sedges, shrubs, trees, ferns, lichens and liverworts and rushes. Functional group diversity was also calculated using the Shannon-Wiener index. Where s is the number of functional groups, P_i is the proportion of species found in the ith functional group expressed as a proportion of total cover and ln is log base$_n$, ranging from 0.62 – 1.89.

Again, functional group richness was the total number of functional groups per sample (2 – 7) and evenness was calculated by dividing Shannon-Wiener index by the natural log of the maximum value Shannon-Wiener's could take (i.e. total functional group richness), ranging from 0.62 – 0.99).

2.3.6.3 Plant biomass and total percentage cover (potential drivers of ecosystem services)

Percentage cover was calculated as the total percentage cover of all species per sample, and ranged from 82.5 – 406 %. Plant biomass was calculated as the total dry mass (g) of all functional groups collected.

2.3.7 Classification

Plant groups were identified using the divisive polythetic classification procedure, Two-Way Indicator Species Analysis (TWINSPAN). Plant communities were classified by hierarchically dividing sets of species or relevés into several related sub-groups using the untransformed Braun-Blanquet percentage cover scores (PC-Ord 5; McCune and Mefford, 1997). The procedure is based on detrended correspondence analysis and, although its use has been criticised due to its poor performance with data sets exhibiting more than one important gradient, (van Groenewoud, 1992; McCune and Grace, 2002), many consider it an effective method of classification for ecological data (Kent and Coker, 1992; Cowlishaw and Davies, 1997; Enright *et al.*, 2005; Parr *et al.*, 2009). The default settings were used.

2.3.8 Multivariate analysis

The main distribution patterns of plants and their relationships with environmental and management factors were explored using the ordination technique, non-metric multidimensional scaling (NMS) using the software package PC-Ord 5 (McCune and Mefford, 1997). NMS has been chosen over other methods as it provides more robust ordinations, resistant to quantitative noise (Minchin, 1987; Enright *et al.*, 2005). It is also well suited to non-normal data and does not require transformation (Clark, 1993; McCune and Grace, 2002). Vegetation samples are arranged in a two or three dimensional space in accordance with the rank order of their ecological similarities. Results were selected on the basis of those NMS plots and solutions which had a minimum number of dimensions and the lowest stress and instability values (McCune and Grace, 2002; Enright *et al.*, 2005).

A random starting configuration with a maximum of six axes, a stability criterion of 0.0005, 50 permutations with real data, 20 iterations to evaluate stability; a maximum number of iterations of 500; an initial stepdown of 0.2 and 50 randomised permutations for Monte Carlo testing were selected. Sørensen (Bray-Curtis) distance measures were used and all plant species occurring in less than 5% of the relevés in an ordination were excluded (Parr *et al.*, 2009). In order to maximise the main component of the variation and the first ordination axis, rotation was applied (Pöyry *et al.*, 2004). Relationships between ordination axes and environmental variables were investigated using Spearman's rank correlations, using SPSS 16.0 (2007) (Aerts *et al.*, 2006; Wilson *et al.*, 2006; Li *et al.*, 2011).

2.3.9 Univariate analysis

To prevent the selection of collinear explanatory variables, variance inflation factors (VIFs) were applied (Zuur *et al*., 2009; Zuur *et al*., 2010). All retained variables had a VIF of less than three (Zuur *et al*., 2010). The linear regression assumption of independence was violated (clear patterns existed between the response variables and spatial variables area, farm and habitat), therefore a linear mixed effects model with residual maximum likelihood estimation (REML) was adopted. Stepwise deletion procedures were used to select each model based on the lowest Akaike's information criterion (AIC). All univariate analyses were performed using R, version 2.14.2 (R Development Core Team, 2012), using the packages 'nlme' (Pinheiro *et al*., 2012) and 'lme4' (Bates *et al*., 2012).

In order to meet the assumptions of normality, the following response variables were transformed: plant species evenness was transformed using the inverse hyperbolic tangent function, as a means of retaining two outlying data points, functional group evenness was arcsine transformed and plant biomass was log transformed. Plant species richness and functional group richness, as count data, were not log-transformed (O'Hara and Kotze, 2010), instead, a Poisson error term was used to analyse patterns, using a GLMM (Bolker *et al*., 2009). The explanatory variables altitude and the percentage of sedges were also log transformed. Raw values of the response variable, total percentage cover, were analysed. The percentage of traditional ewes (4 possible categories), altitude (continuous in metres) and the percentage of sedges were analysed as fixed effects. Habitat (12 levels) was nested within farm (12 levels), which was nested within area (4 levels), and therefore all three factors were treated as random effects.

Model simplification was used to select the minimal adequate model. Models were validated by checking their homogeneity using plots of standardised residuals versus fitted values, as well as standardised residuals versus the explanatory variables used in each model. QQ-plots and histograms of the model residuals were used to assess normality, in conjunction with the Shapiro-Wilk test. REML was used to estimate the random effects terms and Maximum Likelihood (ML) was used to quantify the fixed effects. The likelihood ratio test systematically compared each interaction with the whole model to allow the retention of terms with significant explanatory power (Zuur *et al*., 2009). The AICc, ΔAIC, Akaike weights and evidence ratios were used in decisions regarding two similarly adequate models. The baseline of the percentage of traditional ewes category was changed successively in order to test for differences between all possible categories.

Only parameter estimates and standard errors are reported for the LMMs and GLMMs, as the associated p-values can be unreliable (Baayen *et al*., 2008). The unbalanced nature of the data in the present study and the non-significance of the two-way interaction terms in the majority of models, demonstrated the importance of the main effect terms. Some p-values have been reported in relation to overall effects of particular categorical explanatory variables, using the anova function. When using sequential sum of squares the order of variables in the model is important (Zuur *et al*., 2009; Hector *et al*., 2010), therefore Type III Sum of Squares were adopted. The use of Type III Sum of Squares whilst controversial (Hector *et al*., 2010), was therefore considered justified on this occasion.

2.4 Results

2.4.1 Classification (144 relevés)

TWINSPAN analysis selected clear groupings within the data set, which reflected habitats: 1. improved grassland, 2. all other grassland, 3. blanket bog, 4. heath and 5. scrub. Further division indicated a separation into sub-groups that reflected the communities described by the Braun-Blanquet approach (White and Doyle, 1982), Fossitt (2000) and the National Vegetation Classification (NVC) (Rodwell *et al*., 2000; Elkington *et al*., 2001; Averis *et al*., 2004). In a comparison of these three classification schemes (See **Appendix A S2.7**), it appears that the same plant communities, although independently attained, arise across all three schemes within each TWINSPAN group. The results suggest that, irrespective of the classification scheme adopted, the majority of habitats sampled are mosaics consisting of a variety of different plant communities. Indicator plant species may then be used to inform on the condition of the habitat, which may also suggest the present management regime adopted, accounting for particular environmental variables.

2.4.2 Ordination – Plant composition (144 relevés)

NMS ordination explained 76.7% of the variation in the plant species percentage cover data, with Axis 1 accounting for 46.2%, Axis 2, 14.1% and Axis 3, 16.4% (**Fig. 2.1**). Axis 1 was strongly positively correlated with soil characteristics, such as nitrogen content and soil depth, as well as altitude, % shrubs, drainage and firmness. Axis 1 was most negatively influenced by soil pH, soil moisture content and % grasses (See **Appendix A S2.1**). *Vaccinium myrtillus* and *Erica tetralix* were positively correlated with Axis 1, while grasses *Agrostis canina*, *Agrostis capillaris* and *Festuca vivipara* were all negatively correlated with Axis 1 (**S2.4**). Axis 2 appeared to be most highly influenced by grazing management variables such as % litter and vegetation height (positively) and % dung, % signs of grazing (negatively) (**S2.1**). *Molinia caerulea* and *Ulex gallii* were positively correlated with Axis 2, while grasses *Nardus stricta* and *Holcus lanatus* and the forb, *Galium saxatile* were among the species negatively affected by Axis 2 (**S2.4**). Axis 3 was mainly correlated with habitat richness, % wet heath habitat and slope (positively) and habitat evenness, % dry-humid acid grassland habitat and % lowland blanket bog habitat (negatively) (**S2.1**). *Pteridium aquilinum*, *Calluna vulgaris* and *Erica cinerea* were positively correlated with Axis 3, as was the forb, *Cerastium semidecandrum*, while *Narthecium ossifragum*, *Carex distans* and *Eriophorum angustifolium* were negatively influenced by Axis 3 (**S2.4**).

2.4.3 Lowland plant composition (69 relevés)

The data were split and relevés from the lowlands (< 200m) were analysed separately from relevés collected from the uplands (> 200m). Over 81% of the variation in plant data in the lowlands was explained by three axes. Axis 1 described 47.8% of the variation, Axis 2, 20.5% and Axis 3, 13.2%. Axis 1 was positively correlated with, among other variables, soil pH, soil moisture content and % forb cover, and negatively influenced by soil nitrogen content, soil depth and % shrub cover (**S2.2**). Grasses *Agrostis canina* and *Festuca vivipara* were positively affected, while *Ulex gallii* and *Erica tetralix* were negatively influenced by Axis 1 (**S2.5**). Axis 2 was positively correlated with grazing management variables % dung, % signs of grazing, grazing state and % grasses, and negatively correlated with vegetation height and % litter (**S2.2**). The grasses *Nardus stricta*, *Agrostis capilaris* and *Holcus lanatus* were all positively correlated with Axis 2, while *Molinia caerulea*, *Potentilla erecta* and *Ulex gallii* were negatively affected (**S2.5**). Axis 3 was associated with % scrub and % lowland blanket bog cover (**S2.2**). The forbs *Ranunculus repens*, *Cerastium fontanum* and *Narthecium ossifragum* were solely influenced by this axis (**S2.5**).

2.4.4 Upland plant composition (75 relevés)

Three axes were able to explain 83.2% of the variation in plant composition in the uplands. Axis 1 accounted for 48.9%, Axis 2, 10.4% and Axis 3, 23.9%. Axis 1 was positively correlated with, among other variables, soil pH, soil moisture content and % wet heath habitat and negatively correlated with soil nitrogen content, soil carbon content, soil depth, % sedges, % rushes, % dry-humid acid grassland habitat, % improved grassland habitat, drainage and firmness (**S2.3**). The grasses *Holcus lanatus* and *Agrostis stolonifera* were positively influenced by Axis 1, while *Nardus stricta* was negatively affected (**S2.6**). Axis 2 was positively associated with vegetation height and negatively associated with habitat type and altitude (**S2.3**). The grass *Molinia caerulea*, rush, *Juncus squarrosus* and forb, *Narthecium ossifragum* were positively influenced by Axis 2, while the heather, *Erica cinerea* was strongly negatively influenced (**S2.6**). Axis 3 appears to be highly correlated with grazing management variables, % litter, % mosses and % shrubs (positively) and grazing state, % signs of grazing, % dung and % grasses (negatively). Habitat diversity is also positively correlated with Axis 3, while plant diversity and species richness are negatively correlated (**S2.3**). Species such as the sedge, *Carex echinata*, and the shrubs *Vaccinium myrtillus* and *Calluna vulgaris* were positively affected by Axis 3, while the grass, A*grostis capillaris* was negatively influenced (**S2.6**). Only *Calluna vulgaris* appeared to be equally affected by all these axes.

2.4.5 Soil characteristics

Field observations on heath showed soil depths of between 5 and 35cm (montane heath on mountain tops and wet and dry heath on the steeper slopes). Shallower soils (often < 2cm) were usually found beneath habitats such as dry-humid acid grassland or improved grassland in the lowlands. Deep peaty soils of 30-150cm depth or more were found to support blanket bogs, particularly on the flatter, waterlogged ground. Soil pH decreased from 6.7 (improved grassland in the lowlands) to 4.2 (blanket bog in the uplands), most likely as a result of nutrients leaching on steep ground. Soil depth and nitrogen content increased, from 2 mg/g (improved grassland) to 26 mg/g (blanket bog). The % shrubs, mosses and lichens and % litter were higher on farms with a lower percentage of tradition ewes, while % signs of grazing and % bare ground increased with an increase in management, due to poaching.

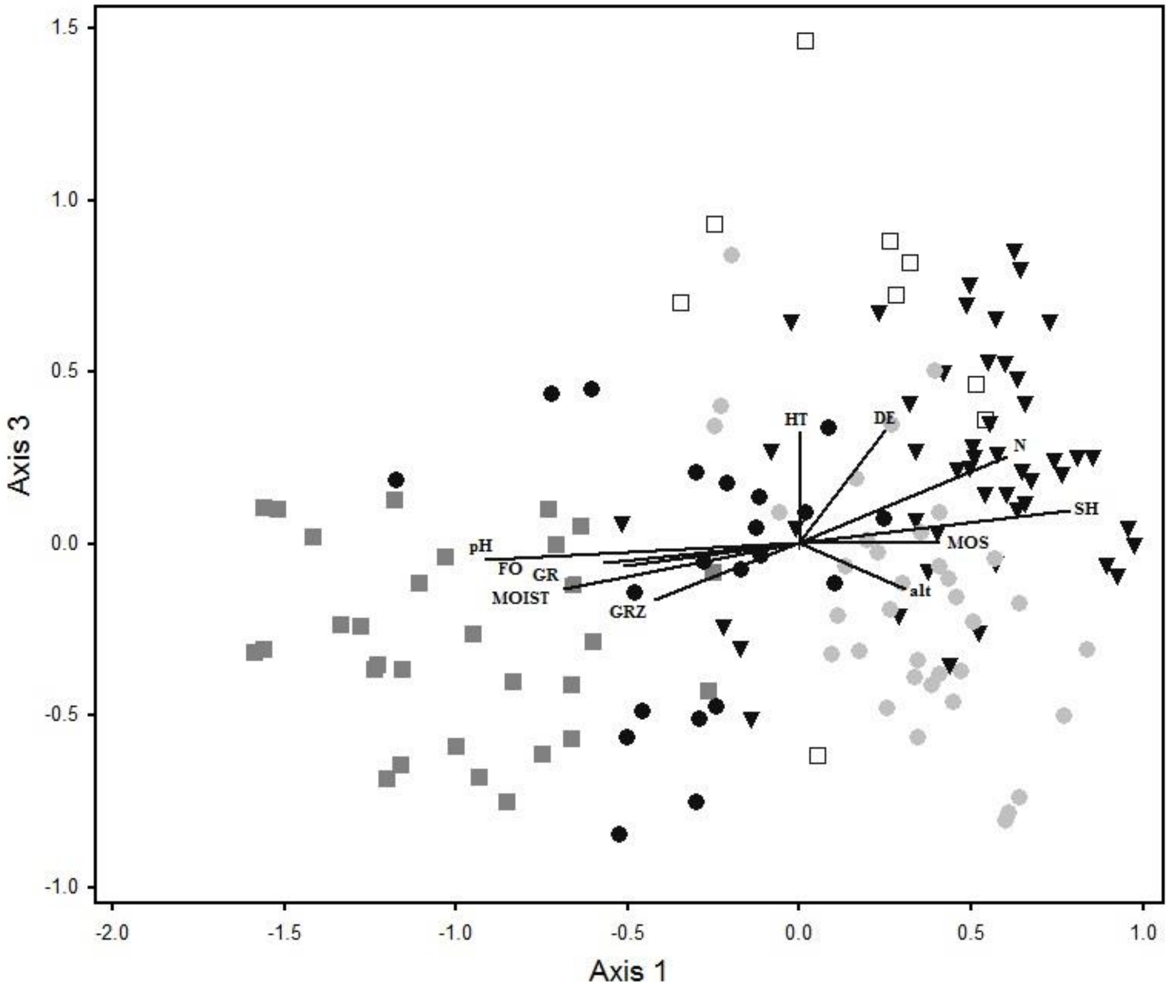

Fig. 2.1 NMS showing the explanatory variables most significantly correlated with axes 1 and 3. ■ = improved grassland, ● = wet grassland and dry humid acid grassland, ▼ = blanket bog, ● = heath, □ = scrub. HT = vegetation height (cm), DE = soil depth (cm), N = soil nitrogen content (mg/g), SH = % shrubs, MOS = % moss, alt =altitude (m), GRZ =% signs grazing, MOIST = % soil moisture, GR = % grass, FO = % forbs, PH = soil pH.

2.4.6 Effect of farm management on plant diversity (144 relevés for all univariate analysis)

Although there was no evidence to suggest an overall effect of percentage of traditional ewes on plant evenness ($F_{3,5}$: 2.93, p = 0.139), farms containing 100% traditional ewes did exhibit significantly higher plant evenness levels than farms containing 0% traditional ewes (estimate 0.140 ± se 0.052) (**Fig. 2.2**).

The results of the linear mixed effects modelling suggested that farms containing a mixture of 50% traditional and 50% commercial sheep breeds actually exhibited the lowest plant species richness, while 100% traditional ewes displayed the highest. Plant species richness was, however, also influenced by the interaction between altitude and the percentage of traditional ewes on a farm (estimate -0.673 ± se 0.281) (**Fig. 2.3**). Farms comprising 0%

traditional ewes contained reduced plant species richness in the lowlands and farms comprising 100% traditional ewes contained reduced plant species richness in the uplands.

There was a positive influence of altitude on functional group evenness (**Fig. 2.4**) and functional group richness (**Fig. 2.5**).

2.4.7 Effect of plant diversity, management or altitude on potential drivers of ecosystem services

2.4.7.1 Plant biomass

There was always a positive effect of altitude on $\log_{10}$ transformation of plant biomass, irrespective of the plant diversity measure in the model (**Fig. 2.6)**:

$\log_{10}$ (plant biomass) ~ atanh (plant evenness) + $\log_{10}$ (altitude) + % traditional ewes (estimate 0.469 ± se 0.166)
$\log_{10}$ (plant biomass) ~ plant species richness + $\log_{10}$ (altitude) + % traditional ewes (estimate 0.480 ± se 0.166)
$\log_{10}$ (plant biomass) ~ asin (functional group evenness) + $\log_{10}$ (altitude) + % traditional ewes (estimate 0.398 ± se 0.164)
$\log_{10}$ (plant biomass) ~ functional group richness + $\log_{10}$ (altitude) + % traditional ewes (estimate 0.404 ± se 0.170)

However functional group richness also had a positive influence on $\log_{10}$ transformation of plant biomass (estimate 0.05 ± se 0.025) (**Fig. 2.7**).

2.4.7.2 Percentage plant cover

The only measure which had a significant effect on percentage plant cover was plant species richness (estimate 8.488 ± se 1.376) (**Fig. 2.8**).

In **Fig. 2.9** the positive influences of environmental and management factors on plant diversity and the potential drivers (total percent cover and plant biomass) of ecosystem services are displayed.

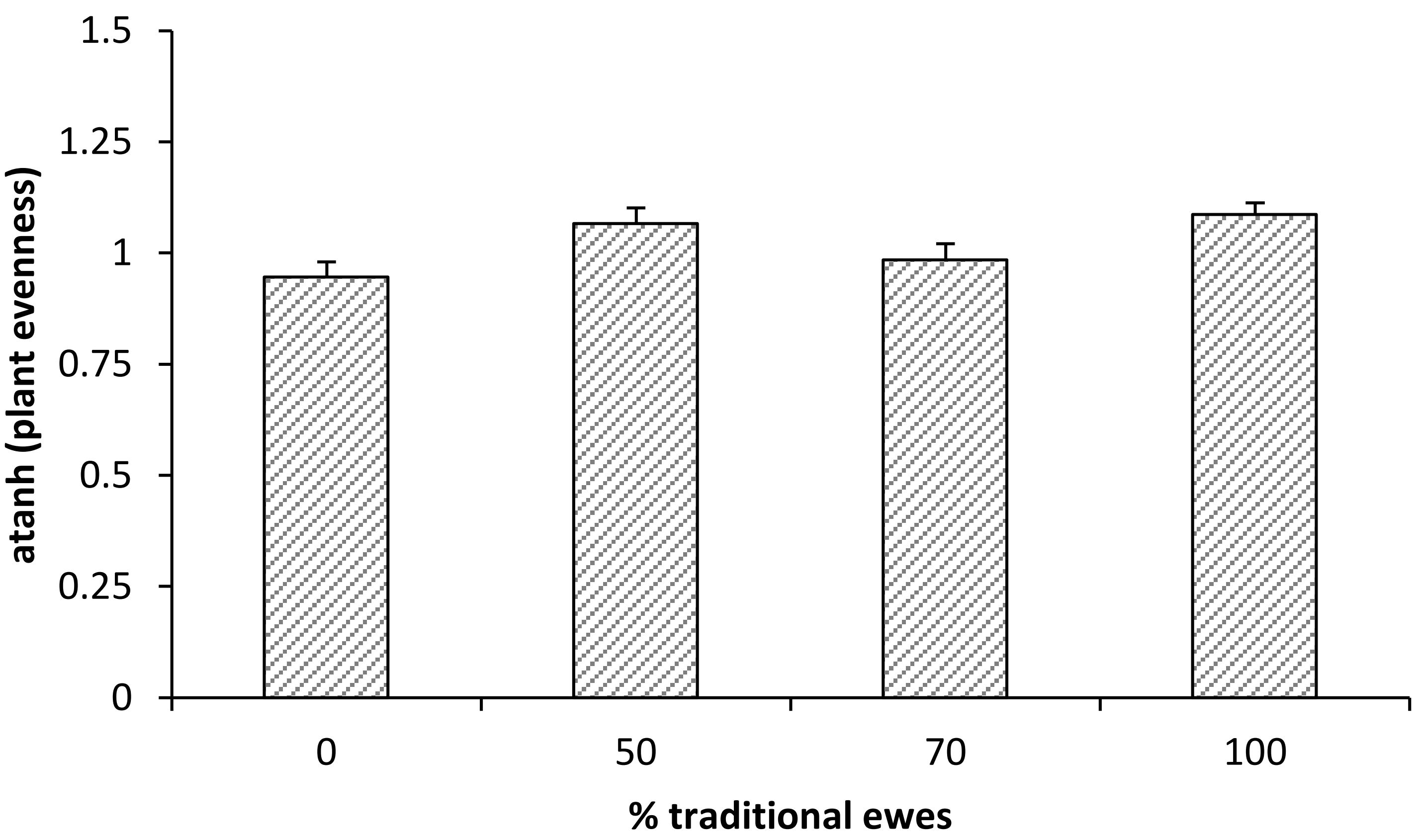

Fig. 2.2 Showing the significant difference in plant evenness between farms with 0% and 100% traditional ewes.

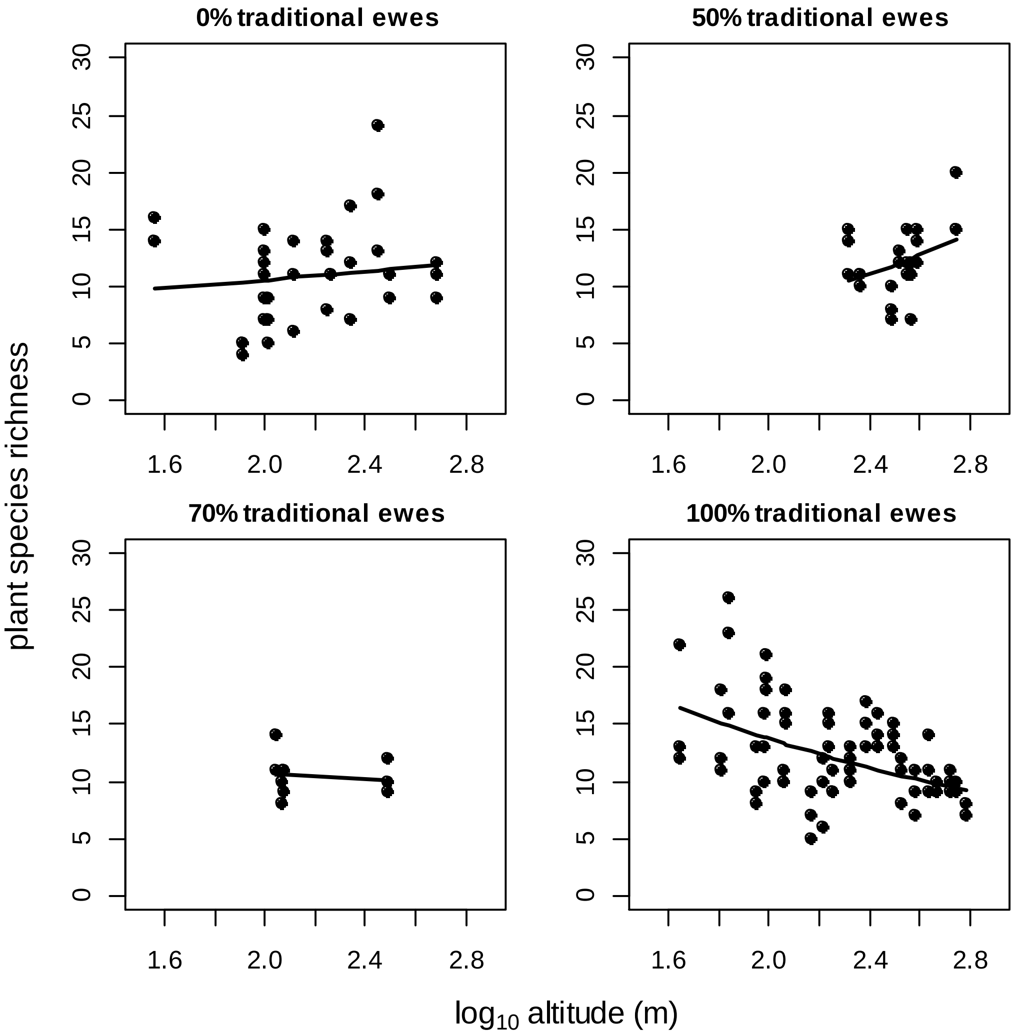

Fig. 2.3 Showing the effect of $\log_{10}$ altitude and percentage of traditional ewes (0%, 50%, 70% and 100%) on plant species richness.

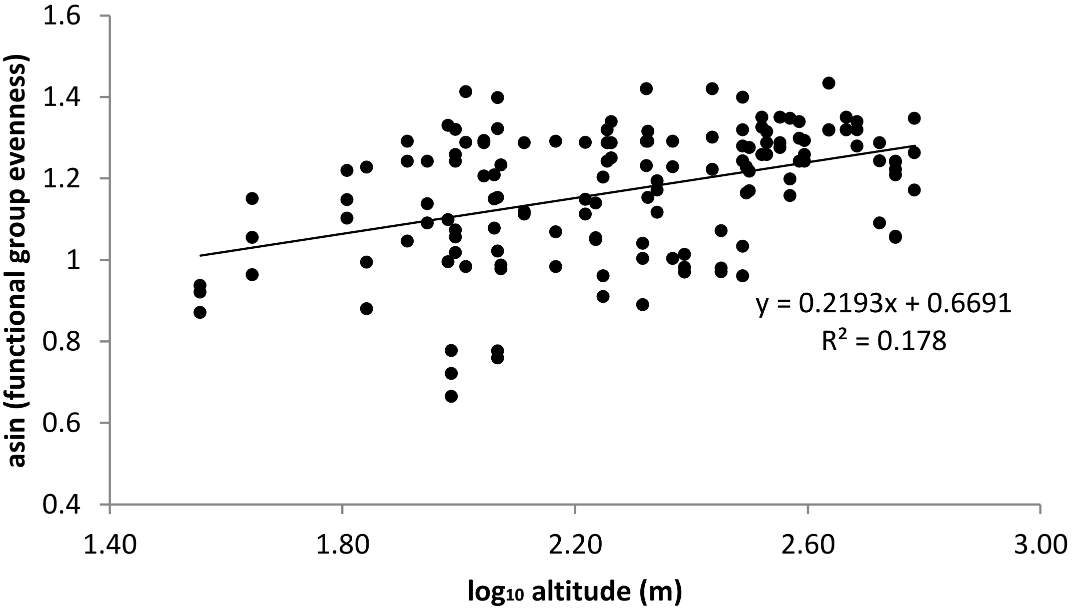

Fig. 2.4 The influence of $\log_{10}$ altitude on functional group evenness.

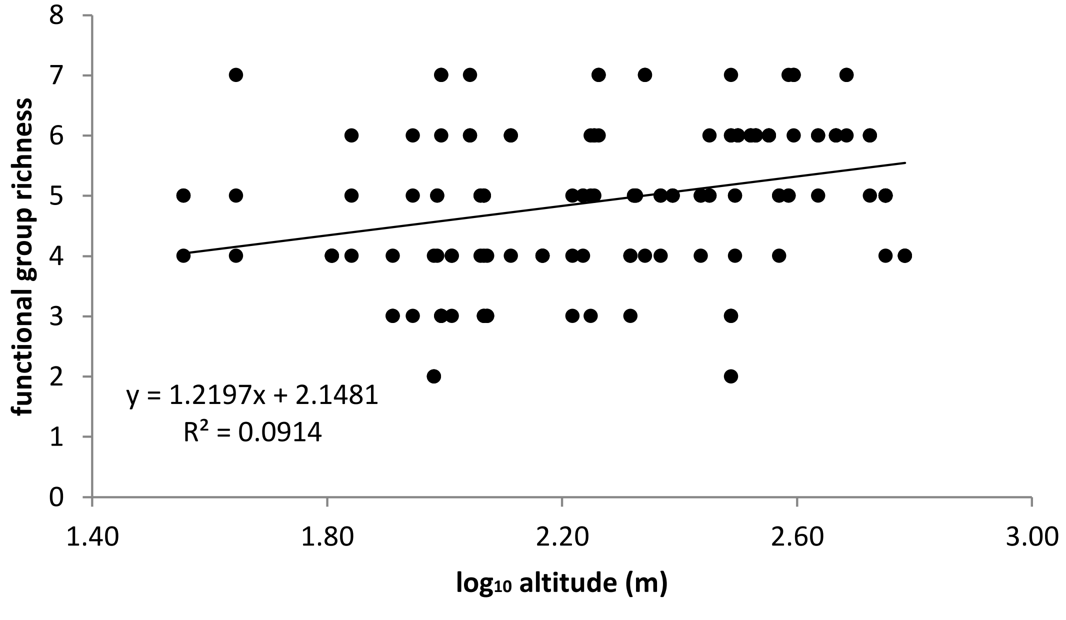

Fig. 2.5 The influence of $\log_{10}$ altitude on functional group richness.

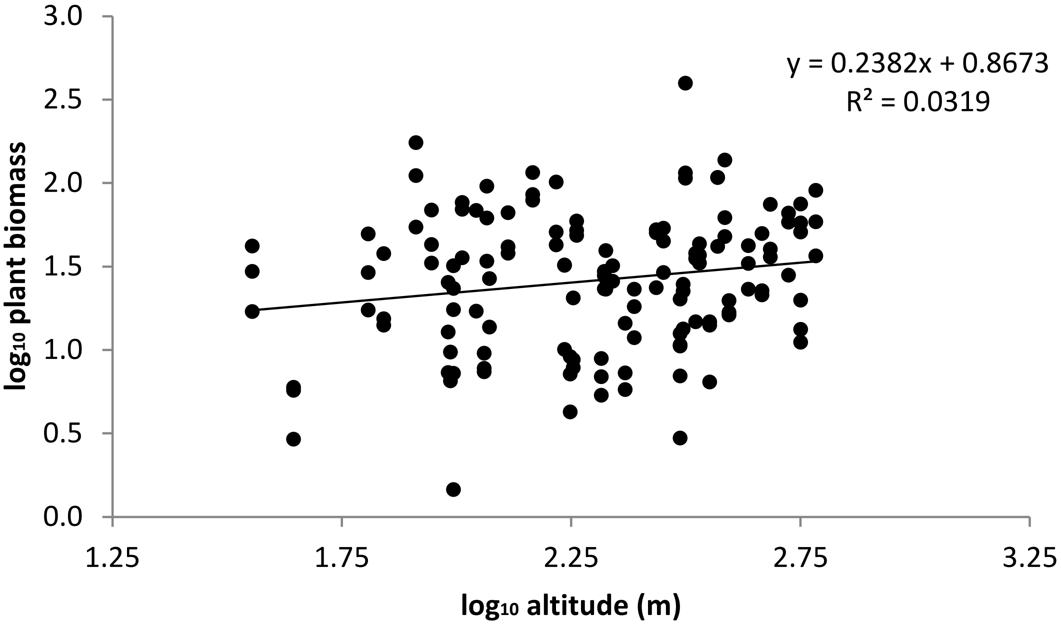

Fig. 2.6 The effect of $\log_{10}$ altitude on plant biomass.

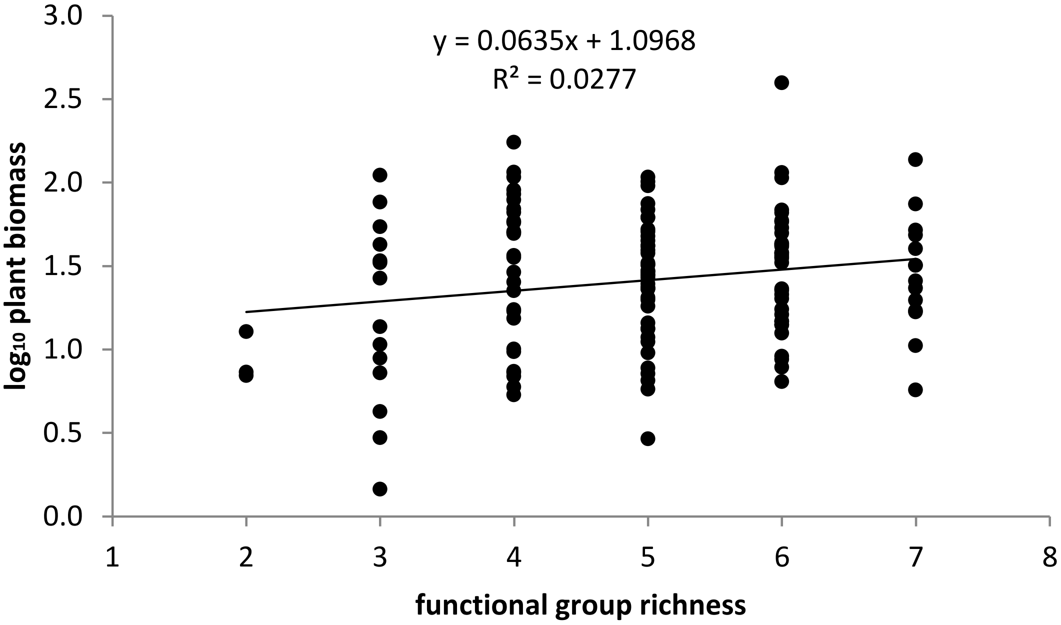

Fig. 2.7 The effect of functional group richness on plant biomass.

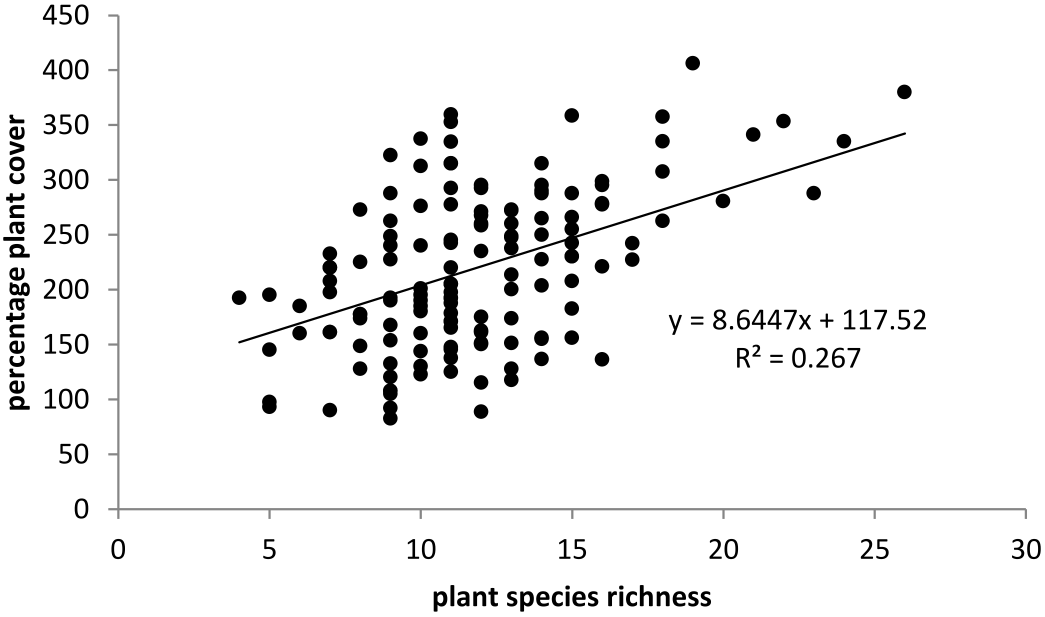

Fig. 2.8 The effect of plant species richness on percentage plant cover.

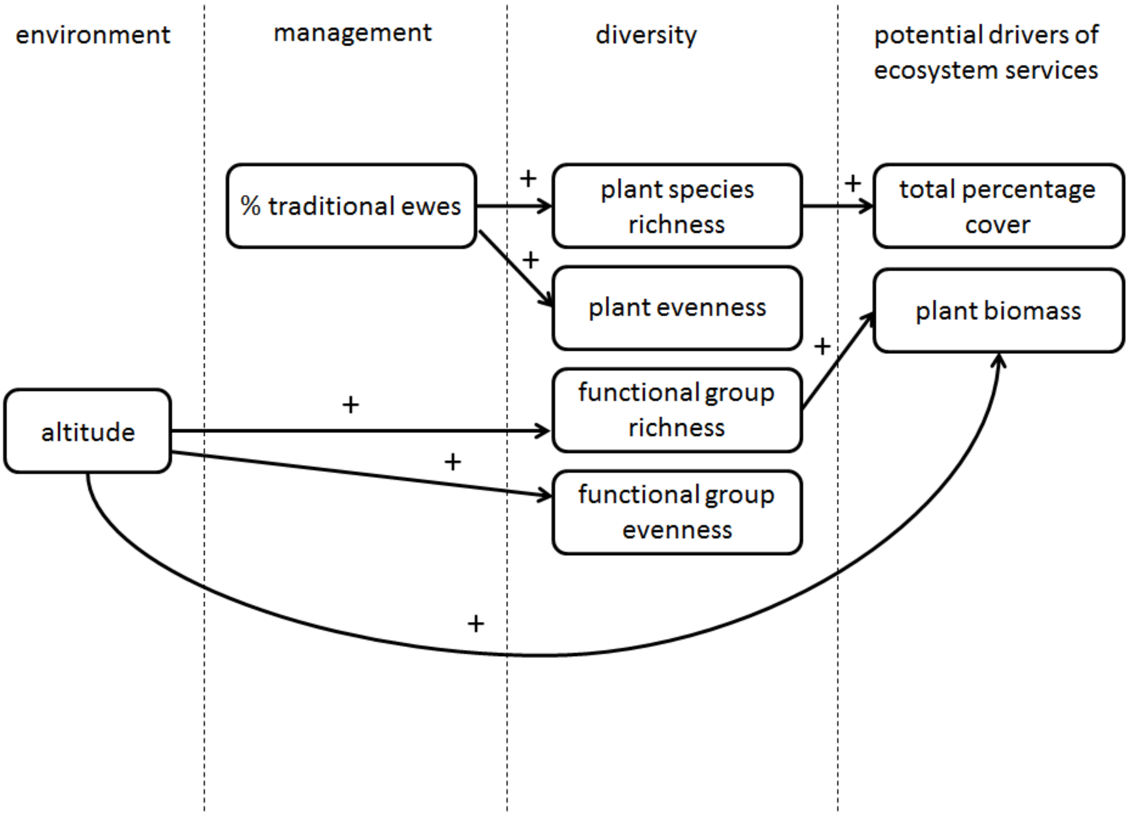

Fig. 2.9 Significantly positive effects of environmental and management factors on plant diversity and potential drivers of ecosystem services.

2.5 Discussion

Previous studies have compared TWINSPAN groupings with NVC groups (Brown *et al*., 1993; Dunford and Feehan, 2001; Parr *et al*., 2009). This study also compared TWINSPAN groups with Braun-Blanquet communities (White and Doyle, 1982) and the Fossitt (2000) classification. As in this study, other work has also found broad habitat differentiations in the first TWINSPAN division. Groups are then divided into Braun-Blanquet associations, characterised by particular indicator species. These groups differ in altitude, also observed by Brown *et al*. (1993), plant composition, species richness, soil characteristics, type of management or management history. Some studies have found that disturbance factors, such as distance to centre of farm (Vandvik and Birks, 2004), may separate TWINSPAN groups. The level of grazing, as determined by percentage cover of certain plant species, was found to vary between TWINSPAN groups in the present study. This finding was supported by Dunford and Feehan (2001). However, others have found no effect of grazing on plant species composition (Allen-Diaz and Jackson, 2000). Perhaps this is because plant composition is slow to change as grazing intensity changes, with the exception of plant communities following complete abandonment (Marriott *et al*., 2004). This approach has shown that there are similarities between the TWINSPAN and the phytosociological classification, suggesting the presence of real patterns in the vegetation. A finding also observed by Vandvik and Birks (2004).

The majority of TWINSPAN groups share species and are therefore perhaps better thought of as a continuum of vegetation types as opposed to discrete vegetation units. NMS was employed to help identify gradients in plant species composition (regardless of whether the focus was on the uplands or lowlands). The present study revealed a soil gradient, with high soil nitrogen content and depth at one end (the uplands, consisting predominately of heathers and other shrubs) and high soil pH and moisture content at the other end (the lowlands, mainly comprising grass species). The second gradient suggested a change in grazing management, with high % litter and vegetation height at one end (representing a low level of management, with *Molinia caerulea* and scrub species such as *Ulex gallii*) and high % dung and % signs of grazing at the other end (representing a higher management level, with grass species such as *Nardus stricta* dominating).

Aerts *et al*. (2006) also found that soil depth and grazing intensity explained differences in plant species composition, while Enright *et al*. (2005) determined that slope was a better indication of plant species richness and composition than soil characteristics or human impact factors. Power and Cooper (1995) also found that soil characteristics explained a large percentage of variation in their data, with axis 2 possibly corresponding with a gradient in soil waterlogging (moisture). They also detected an increase in competitive grass species such as *Lolium perenne* and a decrease in *Calluna vulgaris* as grazing intensified. The findings of Dech *et al*. (2008) concur with those in the present study, inferring that plant species composition could be explained by two axes. One axis was correlated with soil pH and nitrogen levels while the other was associated with litter depth, also found in other studies (Hall *et al*., 2008).

Many studies have found strong effects of soil characteristics on plant species composition; particularly that of soil pH and moisture content (Ogutu, 1999; Lyon and Sagers, 2002; Lu *et al*., 2006; Huebner *et al*., 2007). However others have found that management gradients, such as grazing, have more influence on plant species structure (Perelman *et al*., 1997; Clarke, 2003; Cooper *et al*., 2005; Woodis and Jackson, 2009; Zhang and Dong, 2009). Some have found that both environmental and grazing factors influence plant composition (Ejrnæs and Bruun, 2000; Reinhammar *et al*., 2002). Vandvik and Birks (2002) determined that both grazing and soil factor gradients were important in explaining the variation in plant composition, however, these effects were very much determined by spatial scale. Others have found that a gradient in rainfall can help to determine plant species composition (Anderson and Hoffman, 2007).

Although an altitudinal gradient was detected in the present study, the difference in plant species composition between the uplands and lowlands was small, also reported by Anderson and Hoffman (2007) and Power and Cooper (1995). This may indicate that the west coast of Europe is an extreme environment, even at low altitudes (Thompson and Brown, 1992).

The Braun-Blanquet, Fossitt and NVC classification approaches, along with TWINSPAN analysis, have been used to describe the condition of a particular habitat or plant community in the *present*, using indicator species such as *Molinia caerulea* and *Nardus stricta*. NMS has used these groupings in plant species to help determine what environmental or management gradients may be influencing the data, again in the *present*. Univariate analysis has been used to examine changes in grazing management levels and allows the *future* state of a habitat to be predicted.

Plant species richness would be expected to decline with increasing altitude (Körner, 1999). However the results of the present study appear to show a more complicated scenario. The percentage of traditional ewes may be used as a management gauge for plant species richness or evenness, as findings revealed that a flock comprising of half traditional and half commercial breeds was actually the worst combination in terms of plant species richness. However, species richness is also dependent upon altitude and there appears to be a threshold at around 300m, where farms with 0% traditional ewes and low plant species richness in the lowlands show a slight increase in plant species richness in the uplands, while farms with 100% traditional ewes and high plant species richness in the lowlands show a decrease in plant species richness in the uplands. One possible explanation for this may reflect the distribution of animals across a farm. Farms with 0% traditional ewes may graze their lowland regions fairly intensively, resulting in low plant species richness, while their uplands experience intermediate grazing, giving rise to higher plant species richness. Conversely, farms with 100% traditional ewes perhaps concentrate the majority of their flock in the uplands, where traditional sheep are highly adapted to the unforgiving conditions, resulting in reduced plant species richness in the uplands, while the lowlands experience a lower level of grazing, giving rise to higher plant species richness.

The development of particular characteristics have allowed the adaptation of traditional breeds to local conditions (Wright *et al*., 2002) and there are several instances where traditional breeds have been used to promote biodiversity. On the Isle of Rum, for example, highland cattle have been used to increase plant species richness. However, the majority of evidence is anecdotal (Rook and Tallowin, 2003; Rook *et al*., 2004) and some suggest that any differences in grazing behaviour between breeds can be explained by differences in body size, dental and digestive anatomy (Illius and Gordon, 1987; Rook *et al*., 2004).

Research into grazing has concentrated on the intensity of grazing and the species of grazer, resulting in a major gap in our knowledge of the role of traditional sheep or cattle breeds in farming systems and their influence on the surrounding biodiversity, particularly in the marginal uplands (Wright *et al*., 2000; 2002). There are very few studies in the literature showing variations in the choices made by different sheep breeds (Osoro *et al*., 2002;

Dumont *et al*., 2007). Although it is possible that young animals may learn how to graze from their mothers, so ‘breed’ differences might just be ‘cultural’ (Meg Pollock, pers. comm.).

Some studies have shown that plant community composition was influenced by livestock type, while grazing intensity determined plant species richness (Stewart and Pullin, 2008). This may also be influenced by environmental conditions, which affect the productivity of a system. In fact studies have shown that grazing in more productive environments increases plant species richness, while grazing in low-productive environments decreases plant species richness (Olff and Ritchie, 1998; Proulx and Mazumder, 1998; Pykälä, 2007). Reduced grazing intensity has also been shown to enhance invertebrate diversity on grasslands (Wallis De Vries *et al*., 2007). Scimone *et al*. (2007) found that grazing intensity had a pronounced effect on vegetation structure but there was no evidence to support an effect of traditional breed of sheep or cattle on plant diversity, yet there was a significant effect of cattle grazing intensity on plant species richness in the UK. Dumont *et al*. (2007) found that traditional sheep and cattle breeds were, in general, less selective in their grazing behaviour than commercial breeds. This suggests a greater ability of traditional breeds to exploit low quality forage, although this is most likely due to differences in body size and digestive ability. A moorland study found that Scottish Blackface sheep consumed more *Calluna vulgaris* and later in the season than the other hill sheep breeds, suggesting that land managers may be able to achieve specific environmental goals through their choice of sheep breed (Fraser *et al*., 2009). Scottish Blackface ewes have been found to select acid grassland habitats to the greatest extent and blanket bog the least (Williams *et al*., 2012). Celaya *et al*. (2010) also found differences in browsing behaviour between traditional and commercial goat breeds, significantly affecting the composition and structure of the heathland, with sites grazed by the traditional breed exhibiting greater plant species richness. Other studies have found no influence of livestock breed on plant composition (Hessle *et al*., 2008) or diversity (Rook *et al*., 2006; Scimone *et al*., 2007; García *et al*., 2009), or animal diversity (Wallis De Vries *et al*., 2007). There is also evidence to indicate that traditional breeds have no advantage, in terms of production, over commercial breeds on extensively managed pasture (Isselstein *et al*., 2007). The economic performance of traditional breeds is also generally regarded as poorer due to marketing difficulties (Rook *et al*., 2006). Although perhaps the reconnection with local culture and food networks may provide a market advantage (Mills *et al*., 2007).

A farm management survey conducted in conjunction with the present study area examined 72 farms (including the twelve described here). The results indicated that although 58% of the total flock (from 72 farms) consisted of traditional Scottish Blackface ewes, 42% consisted of traditional ewes which were cross-bred with lowland sheep breeds such as Texel, Charollais and Suffolk due to current market demands for heavier lambs (Kramm *et al*., 2008; O'Rourke *et al*., 2012). The farmers acknowledged that the cross-bred sheep were not as well suited to the harsh conditions of the mountains as the traditional Scottish Blackface sheep and required supplementary feeding. This suggests that there is a trade-off between spending money on imported feedstuff but achieving a better price per lamb and saving money by not buying feedstuff but achieving a lower price for each lamb. Results also revealed that farms containing a higher proportion of good grazing or 'green-land' in the lowlands generally had shorter upland grazing seasons than farms with less 'green-land'. The latter comprised the highest percentages of traditional ewes, grazed the uplands for the majority of the year and subsequently had lower incidences of upland scrub encroachment (Kramm *et al*., 2008; O'Rourke *et al*., 2012).

Petchey and Gaston (2006) define functional diversity as the variety of ways in which a species or an ecosystem can respond to change. Functional group richness and evenness, in the present study, were not influenced by percentage of traditional ewes, however, they were both positively affected by altitude. This may be the consequence of sewing non-native grasses, the application of fertiliser or the drainage of 'green-lands', which result in the domination of one or two functional groups such as grasses or rushes in the lowlands. However, this finding is contrary to other studies which found that plant functional diversity decreased with altitude, following a similar pattern to plant species richness (Rahbek, 1995), although the distributional limits of each functional group were well defined along the altitudinal gradient (Pavón *et al*., 2000). Others have also found that animals follow a similar pattern, as functional spider diversity decreased with altitude (Cardoso *et al*., 2011). It was suggested that this may be linked to lower habitat complexity in the uplands. Others have found that altitude was only able to explain a small portion of the variation in plant functional diversity (Brinkmann *et al*., 2009). Some looked at the effects of altitude on individual plant functional groups and found that different groups exhibited various responses to environmental gradients (Bruun *et al*., 2006; Zhang and Zhang, 2007). It may be that in the present study factors such as steepness, precipitation, humidity, historical management or regional effects influenced the plant species to a greater extent than any negative factors associated with high altitudes, such as a reduction in temperature and a corresponding loss in productivity (Rahbek, 1995). However, it should be pointed out that many of these studies are conducted at much higher altitudes, with plant functional diversity peaking at around 400m or higher, an elevation which is often at the limits of many of the farms in the present study.

Plant biomass was positively affected by functional group richness and by altitude, albeit weakly. Higher biomass in the uplands may reflect lower decomposition rates perhaps due to cooler and wetter conditions (Kueppers *et al*., 2004). It may also indicate a general trend in undergrazing of the uplands. Research has shown that the strength of the effect of altitude on biomass varies with plant functional group but there is generally a reduction in biomass with altitude (Liao *et al*., 2011). In a compilation of various alpine studies Körner (1999) found that above-ground live plant biomass decreased with increasing altitude, however he attributes this to the short growing season at high altitudes and the decrease in land cover (high rock cover), as opposed to an actual decrease in biomass itself. In fact, he states that the amount of dead plant material actually increases with altitude. The combination of live and dead plant material (total biomass) in the present study may explain why an increase in biomass with altitude was recorded, with the high proportion of dead plant material in the uplands increasing the total biomass, possibly again reflecting the lack of grazing in the uplands. In the present study plant species richness was found to decrease as biomass increased, however this was not significant. Gough *et al*. (1994) also found a reduction in species richness with an increase in biomass, although this was a very weak relationship and concluded that biomass is a poor predictor of species richness. Perhaps the greater the plant biomass, the higher the possibility of encountering many functional groups, the majority of which, however, only contain a few competitive species, thereby reducing plant species richness. Lower plant species richness may attract fewer invertebrates and therefore fewer bird species, so overall diversity would be likely to fall (Dennis *et al*., 2002; 2008).

As in the present study, previous work also found that biomass increased with functional group richness (Hector *et al*., 1999; Spehn *et al*., 2005; Lanta and Lepš, 2006), while others found that plant composition explained more of the variation in primary productivity (biomass) than functional group richness (Hooper and Vitousek, 1997). Others have found similar positive effects of functional group diversity on litter decomposition, important in nutrient cycling and productivity (Scherer-Lorenzen, 2008). Tilman *et al*. (1997) used biomass as a measure of productivity and, as in the present study, found that functional diversity had a stronger impact on ecosystem processes than species diversity. They found that composition had a large impact on ecosystem processes, suggesting that the loss or gain of individual species with certain functional traits may have strong positive or negative effects on an ecosystem. Jiang *et al*. (2007) also found that functional group diversity was more important than species diversity in predicting ecosystem functioning. This may be because areas with higher functional diversity will include species with a wider variety of traits, allowing the more efficient use of resources (Petchey and Gaston, 2002; Petchey *et al*., 2004).

Plant species richness was found to have a positive effect on total percentage cover in the present study, this may help to prevent poaching and erosion by providing protection for understory vegetation (Brewer *et al*., 1997). Previous studies have also found that plant cover increased with species richness (Tilman, 1997; Huntsman, 2011). Although plant species richness may decrease if the plant cover contains a high proportion of invasive species (Alvarez and Cushman, 2002). This was also observed in marine invertebrates, where high native species richness reduced the percentage cover of invading invertebrates (Stachowicz *et al*., 2002). This suggests that diverse communities decrease invasability, particularly at small scales, through resource competition (Knops *et al*., 1999; Naeem *et al*., 2000; Knight and Reich, 2005). High plant cover may also attract many animal species. Rango (2012), for example, found that ant species richness was positively correlated with plant cover, perhaps as a result of the increased shelter and shade provided. However, the removal of some plant cover can also be beneficial, as it enhances seedling emergence (Lenssen *et al*., 1999). Allen-Diaz and Jackson (2000) found that total vegetative cover was a more useful gauge of ecosystem health than plant composition, as vegetative cover was sensitive to increased grazing intensities, particularly under varying weather conditions, such as rainfall. This is important when considering the state of an ecosystem, as vegetative cover has been shown to be directly related to erosion rates (Busby *et al*., 1994) and both wild and domestic animals can influence soil processes (Pastor *et al*., 1988; Whicker and Detling, 1988). Although altitude was not retained in the percentage cover model in the present study, a negative relationship was found between percentage cover and altitude, although it was not statistically significant. Anderson and Hoffman (2011) also found that although overall percentage cover decreased with altitude, the inclusion of grazing intensity in the analysis resulted in a decrease in percentage cover in the lowlands and a corresponding increase in the uplands. A loss in perennial shrubs may explain the lowland decrease (Anderson and Hoffman, 2007), while an increase in annual species, which proliferate under heavy grazing may explain the upland increase (Díaz *et al.*, 2007).

It has been suggested that stocking rates often give a poor indication of grazing pressure in the uplands (Armstrong and Milne, 1995; Grant and Maxwell, 1988) and intensive herding of sheep in certain areas may lead to scrub encroachment in others (Fonderflick *et al.*, 2010). Agri-environment schemes based solely on blanket stocking rates, which disregard local site conditions, are unlikely to display an increase in plant diversity (Mills *et al.*, 2007). Some argue that management based on sward height may provide a more refined measure of grazing pressure (Rook and Tallowin, 2003). Sheep grazing and trampling have been associated with larger impacts on vegetation than those associated with wild herbivores, which tend to have a more local effect (Albon *et al.*, 2007). However, grazing animals do have an important role to play in maintaining structural heterogeneity and floral diversity through processes such as selective defoliation, treading, nutrient cycling and propagule dispersal (Rook and Tallowin, 2003). It has also been suggested that a decrease in sheep numbers on the hills may lead to an increase in numbers of other herbivores such as red deer (*Cervus elaphus*) (Albon *et al.*, 2007) or field voles (*Microtus agrestis*) (Steen *et al.*, 2005; Evans *et al.*, 2006). However the only vole species present in Ireland is the bank vole (*Myodes glareolus*) (Yalden, 1999), whose diet differs to that of sheep and as they are also not influenced by elevation, will be unlikely to affect upland sheep grazing (Steen *et al.*, 2005; Torre and Arrizabalaga, 2008). At low densities feral goats (*Capra hircus*) may be able to fill a food niche not occupied to any real extent by livestock species or red deer (Bullock, 1985). Some studies have shown that the return of cattle (*Bos taurus*) to the hills would result in high levels of plant diversity (Lanta *et al.*, 2009; Dumont *et al.*, 2009; Humphrey and Patterson, 2000), as well as in the lowlands (Pykälä, 2003), owing to the less selective nature of their grazing (Pykälä, 2007). On moorland, cattle have been shown to consume significant quantities of invasive grasses such as *Nardus stricta* and *Molinia caerulea* (Grant *et al.*, 1985; Armstrong *et al.*, 1997; Fraser *et al.*, 2009b). Others, however, have found no effect at all of cattle grazing (Jewell *et al.*, 2005). Grazing by traditional livestock breeds has often been suggested as a conservation management tool (Tolhurst and Oates, 2001) owing to their ability to survive harsh environmental conditions (D'hour *et al*., 1998), their greater resistance to parasitism (Jones *et al*., 2006), and skill at exploiting patches of low quality forage (Dumont *et al*., 2007). Some have suggested that through their poorly adapted dietary choices, commercial breeds may actually threaten biodiversity (Dumont *et al*., 2007), while others have found that commercial cattle breeds may provide environmental benefits similar to those produced by traditional breeds (Fraser *et al*., 2009a). Foraging behaviour may also determine vegetation structure and composition. Different herbivore species exhibit different temporal and spatial grazing patterns which effect the vegetation in a variety of ways (Milne, 1996). The highly social nature of sheep has, in itself, been shown to influence grass patch selection (Sibbald *et al*., 2008). Cattle no longer graze the hills in the present study. Feral goats and Irish hare (*Lepus timidus hibernicus*) were present and red deer, although only on those farms bordering Killarney National Park. However, it is unlikely that any of these herbivores were present in sufficient numbers as to influence grazing management.

This study has shown that grazing management does have an effect on plant species richness and the percentage of traditional ewes may be a valuable tool used to gauge this effect, however it is evidently dependent upon altitude, which must always be taken into account. Plant species richness, in turn, positively influenced total percentage cover. Functional group diversity and plant biomass, however, were influenced to a greater extent by environmental factors, particularly altitude. Mills *et al*. (2007) concludes that the key to achieving sustainable grazing systems with high biodiversity is financial assistance to farmers and land managers and clear goals for agri-environment schemes. Biodiversity is now valued as a 'public good' and therefore this may indeed be possible.

2.6 Conclusions

In conclusion, grazing management (as defined by the proportion of traditional to commercial sheep breeds) clearly plays a role in determining plant diversity (species richness and evenness), however it does not appear to influence functional group diversity (richness and evenness), or potential drivers of ecosystem services (plant biomass and total percentage cover), which are more directly affected by altitude. Nevertheless, there was an impact of plant diversity (plant species richness) and functional group diversity (functional group richness) on total percentage cover and plant biomass, respectively. This suggests that it is possible to farm for plant diversity, however it is not possible to farm directly for drivers of ecosystem services or measures of ecosystem functioning. Nonetheless, by farming for biodiversity, drivers of ecosystem services may be indirectly influenced in a positive way. Grazing is often seen as the main driver of plant diversity and heterogeneity in grasslands and therefore appropriate grazing management is crucial (Scimone *et al.*, 2007). If sustainable grazing is used as a means of maintaining or enhancing plant diversity, it is essential that each management plan is adapted to local conditions (Metera *et al.*, 2010).

2.7 Acknowledgements

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Chapter 3

Effects of grazing management and altitude on carabid abundance, diversity, assemblage and ecosystem services

Roslyn M. Anderson, John O'Halloran and Mark C. Emmerson

Carabus clatratus (Photo: Roz Anderson).

3.1 Abstract

Grazing provides an effective tool in the management of marginal land across Europe, particularly in the uplands. Carabid beetles are good indicators of habitat heterogeneity and quality and are therefore a valuable means of disentangling the factors that influence these ecosystems. Carabid beetle abundance, species richness and assemblage composition, as well as Staphylinidae and other beetle abundance were studied to assess their response to a variety of livestock grazing regimes, altitudes and other environmental factors such as soil moisture. The effects of carabid abundance, species richness and consumption rates on soil organic carbon (SOC) were also examined. Beetles were collected from 12 farms in County Kerry in the southwest of Ireland over the spring/summer and summer/autumn of 2007. Univariate analysis was conducted using linear mixed effects modelling (LMM), while the ordination technique Non--metric Multidimensional Scaling (NMS) examined variation in the composition of carabid beetle assemblages, as well as the functional feeding groups of generalist and specialist predators and phytophagous species. Differences across widely varying habitats, including acid grassland and blanket bog, were accounted for by assigning habitat type as a random effect in the LMM. Analysis showed that grazing management and environmental factors played a significant role in determining carabid abundance, species richness and community composition and this was influenced by composition of feeding groups within the carabid assemblage. The study highlighted the effect of grazing management and environmental factors on SOC. However, it also found that carabid abundance, species richness and consumption rate were influential in explaining differences in SOC. At the habitat level the grazing state and altitude interaction was able to help explain differences in beetle abundance and species richness, whilst, at the farm level this interaction also relied upon factors such as soil moisture or % scrub. The present study has revealed the importance of grazing management, in conjunction with site-specific environmental factors, for carabids, staphylinids and other beetles. However, it has also highlighted the fact that changes in carabid beetle abundance and species richness can influence ecosystem functions such as the provision of food for birds, as well as the organic carbon in the soil. Soil organic carbon levels might suggest a potential impact on the ecosystem service of carbon sequestration.

3.2 Introduction

3.2.1 Background

Prior to the 1970s, across Ireland and Britain, both cattle and sheep grazed the hills, however these mixed grazing systems gave way to sheep-dominated management (Fuller and Gough, 1999). Fuelled by subsidy payments, hillsides were commonly overgrazed, leading to the degradation of habitats. Recent European agricultural policy has resulted in the decoupling of subsidies from production, and has led to significant changes in upland farming. In particular, a decline in sheep numbers has led to growing concern that upland biodiversity is now under threat from undergrazing and abandonment (Cole *et al*., 2010).

Throughout Europe, the intensification and abandonment of traditional farming practices has resulted in the loss of priority habitats for conservation, such as heather moorland or semi-natural grassland (Bignal and McCracken, 1996; 2000). In fact the conservation value of upland acid grasslands is often overlooked in favour of that of moorlands (Thompson *et al*., 1995; Dennis *et al*., 2008; Littlewood, 2008; Cole *et al*., 2010). High Nature Value (HNV) upland habitats are managed through extensive grazing in Europe (Cole *et al*., 2010), which help to promote habitat heterogeneity, through the effects of selective grazing, trampling and defecating. The contribution of cattle and sheep help to promote biodiversity and support richer arthropod communities (Tscharntke and Greiler, 1995; Dennis *et al*., 2002; Cole *et al*., 2010), as well as benefitting plants (Pykälä, 2003) and birds (Dennis *et al*., 2008).

3.2.2 Carabids, staphylinids and other beetles

Arthropod species comprise the majority of taxa in the uplands and are critical in upland food chains (Dennis, 2003). Although in upland systems crane flies (Diptera: Tipulidae) predominate over Coleoptera (Coulson, 1988). When lowland grasslands are under intensive management, the semi-natural grasslands of the uplands provide an ideal habitat for beetle species (Dennis *et al*., 1997). Ground beetles (Coleoptera: Carabidae) are one of the most common families of surface-active arthropods in agricultural ecosystems (Cole *et al*., 2002). They are a well-studied family and are sensitive to structural heterogeneity and land use (Thiele, 1977; Lövei and Sunderland, 1996; Niemelä, 1996; Dennis *et al*., 1997; 2002; Ribera *et al*., 2001; Brose, 2003b). Usefulness of carabids in assessing and monitoring change in habitats is well established (Eyre and Rushton, 1989; Blake *et al*., 1996).

Different species may favour particular habitat types and often a better understanding of communities can be achieved through the classification of assemblages based on their ecology (Cole *et al*., 2002). Functional groups, such as generalist or specialist predators or phytophages are influenced in different ways by management and environmental factors (Lövei, 2008). Specialist carabids, in having a narrow range of food resources, may have greater potential to regulate agricultural pest species, while generalists can suppress pest outbreaks but not control them (Lövei and Sunderland, 1996; Mair and Port, 2001). Indeed, large carabids of the *Carabus* genus are adversely affected by intensive management practices (Luff and Rushton, 1989; Rushton *et al*., 1989; Blake, 1996; Ribera *et al*., 2001; Cole *et al*., 2002, 2005), particularly those of cattle grazing (Butterfield *et al*., 1995). Specialist carabid predators, such as *Notiophilus* spp., which specialise on Collembola, hunt using visual cues and therefore prefer a more open sward (Cole *et al*., 2006). Staphylinid species composition may differ substantially from that of carabids, as they favour wetter soil with a high organic matter content (Dennis, 2003), as well as litter and moss which accumulate under low levels of grazing (Good and Giller, 1991). However, they are also associated with dung (Coulson, 1988; Dennis *et al*., 2004).

3.2.3 Grazing management

Livestock grazing is the primary form of management of the uplands. The effects of grazing management on arthropods vary but the majority of studies indicate that the abundance and diversity of arthropods increase under reduced levels of grazing (Dennis *et al*., 1998; 2001; 2004; 2008; Pöyry *et al*., 2006). Effects are generally indirect and occur through changes in botanical composition or vegetation structure (Dennis, 2003). Conversely there is also evidence to suggest that a lack of grazing can be detrimental to arthropods (González-Megías *et al.*, 2004; Debano, 2006). Plant species and functional diversity have also been shown to influence carabids, particularly phytophages such as *Amara* spp. (Tscharntke and Greiler, 1995; Harvey *et al*., 2008).

3.2.4 Spatial scale

The scale at which large grazing herbivores affect carabids depends on several factors, such as the non-uniform grazing behaviour of livestock or the response of plant communities to grazing under varying hydrology, climate or topography (Dennis, 2003). Ground and rove beetles, for example, can roam over tens of metres. Typically, invertebrates, as a result of their susceptibility to changes in microclimate, perceive changes in their environment at finer spatial scales than larger organisms, which potentially make them good indicators of fine-scale changes in habitat heterogeneity (Dennis *et al*., 2002; Cole *et al*., 2010). These fine-scale habitat requirements vary with seasonal and circadian activity patterns, for example, some carabid species hunt in short grass, while seeking refuge in taller grass (Butterfield *et al*., 1995). The larval stage of carabids is also key in their preference for habitats (Lövei and Sunderland, 1996). In fact, soil factors such as moisture content are extremely important in carabid habitat selection (Gardner, 1991; Rushton *et al*., 1991; Bhriain *et al*., 2002; Dennis, 2003), and soil pH in prey availability (King and Hutchinson, 1976). The surrounding landscape too plays a role in explaining invertebrate distribution, although the extent of this influence is determined by body size, diet and mobility (Weibull and Östman, 2003; Holland *et al*., 2005; Schweiger *et al*., 2005).

3.2.5 Ecosystem functioning and services

Grazing is the most geographically expansive land use in the world, occurring on over a third of the earth's surface (Liu *et al*., 2012). Although livestock are known to emit large amounts of methane, and to a lesser extent carbon dioxide, early indications of recent research suggest that traditional cattle breeds emit less methane per kilo of beef produced than commercial breeds (Waterhouse *et al*., 2011). The right type of grazing may therefore have the potential to sequester a large proportion of greenhouse gases as carbon in the soil, thereby helping to mitigate climate change (Scurlock and Hall, 1998), although there is disagreement surrounding the effects of climate change on global carbon stocks (Davidson and Janssens, 2006). Ireland has a large percentage of the world's peatbogs (Cross, 1989), which are not only a substantial store for carbon but are also a large potential sink of atmospheric carbon (Worrall and Evans, 2009; Szyszko *et al*., 2011). One of the most important terrestrial pools for carbon (C) storage and exchange with atmospheric CO_2 is soil organic carbon (SOC) (Follett, 2001; Gupta and Sharma, 2013). By optimising agricultural management for the accumulation of SOC, atmospheric CO_2 may be sequestered, partially mitigating the current increase in atmospheric CO_2 (West and Post, 2002). The impact of insects on ecosystem services such as carbon dynamics are not well documented (Volney and Fleming, 2000; Kurz *et al*., 2008). Invertebrates usually have ten times the concentration of nutrients in their bodies relative to the vegetation in which they live and are hence crucially important in the recycling of nutrients in nutrient poor habitats such as peat bogs

(Coulson *et al.*, 1995). Changes in the ecological composition of carabid assemblages may have knock-on effects on ecosystem functioning, such as the provision of prey for many declining upland bird species (Dennis, 2003; Cole *et al.*, 2002; Buchanan *et al.*, 2006).

It is important to disentangle the direct or indirect effects of grazing management on ground beetles from those of landform (Dennis, 2003). Very few studies have been conducted on the response of invertebrates to grazing management (Mysterud *et al.*, 2010), and only a handful of studies have been conducted on the terrestrial, ground-dwelling invertebrates of Irish mountains (McCormack *et al.*, 2006; 2009), or the effects of invertebrates on ecosystem services such as soil carbon sequestration (Volney and Fleming, 2000; Kurz *et al.*, 2008). This study therefore played a valuable role in contributing to several areas of limited ecological research. Here we investigated the role played by carabid abundance, species richness and assemblage composition (as well as staphylinid and other beetle abundance) of hill sheep farms in mediating ecosystem services such as carbon sequestration. In particular, we focussed on the interplay between (i) grazing management and (ii) environmental factors such as altitude and soil characteristics as determinants of carabid diversity and hence their roles in the delivery of ecosystem services such as carbon sequestration (**Fig. 3.1**).

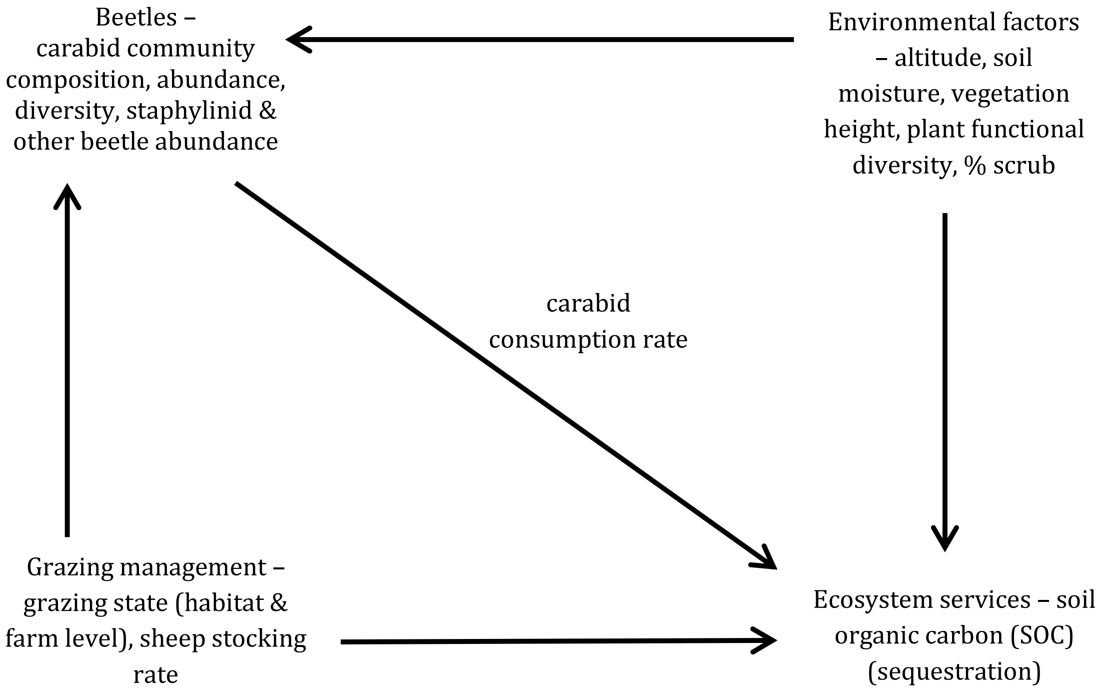

Fig. 3.1 Schematic representation of factors which may influence beetle diversity and ecosystem services.

3.3 Methodology

3.3.1 Study area

The study was undertaken on the Iveragh Peninsula (51° 94´ N, 9° 89´ W), County Kerry, southwest Ireland. The 1400km^2 peninsula is relatively isolated and approximately 65% is classified as upland (O'Rourke and Kramm, 2009; Crowley and Sheehan, 2009). The region is characterised by blanket bogs and heaths, with an abundance of nutrient deficient peaty podzols and blanket peats and an annual rainfall of over 1500mm, (Carruthers, 1998; Averis *et al*., 2004; Crowley and Sheehan, 2009). Harsh weather and poor growing conditions in these marginal areas restrict land use but do provide valuable grazing for hill sheep farming.

As a representation of upland grazing conditions across the peninsula, four geographically distinct areas were selected. Three hill farms of varying grazing intensity were then identified within each area, to give 12 study farms in total. Study farms were generally less than 250ha in size and reached elevations of between 400m and 800m. Sheep stocking rates for the farms ranged from 0.06 – 0.76 LU/ha (livestock units per hectare) and 0.005 – 0.48 LU/ha in the uplands (above 200m).

3.3.2 Grazing state classification – farm and habitat levels

All habitats were mapped on an initial visit to each farm (Fossitt, 2000; Hill *et al*., 2005), with a substantial area consisting of blanket bog and acid grassland. Each farm comprised a heterogeneous mosaic of habitats and grazing intensities. The standard methodology of MacDonald *et al*. (1998) was adopted as a means of quantifying the impacts of grazing, browsing and trampling by large herbivores in upland habitats. Directly observable, habitat-specific field indicators, including the accumulation of dead plant material (litter), cover of bare ground, selectivity of grazing and presence of dung were assessed, using replicated relevés (n = 3 for each habitat type). Light, moderate and heavy (L, M and H, respectively) impact categories were assigned to each field indicator, thus allowing the evaluation of grazing state per habitat and consequently per farm. To account for spatial heterogeneity, a method of summarising grazing impact across habitats was devised, using the percentage of the area occupied by each impact class (Agresti, 1984; Brewer *et al*., 2004; Albon *et al*., 2007). This resulted in the smoothing of the three class impact scale into a more continuous five point scale by the introduction of intermediate classes light/moderate (L/M) and moderate/heavy (M/H), (after Albon *et al*. 2007). Sheep stocking rate was also examined as a measure of grazing management. Category 1 was 0 – 0.2 LU/ha, category 2 was 0.21 – 0.4 LU/ha, category 3 was 0.41 – 0.6 LU/ha and category 4 was 0.61 – 0.8 LU/ha.

3.3.3 Soil sampling

The average soil depth (cm) was calculated by taking measurements at each of the four corners of the relevé. Walking in a 'W' pattern (Tytherleigh and Peel, 2003; Marriott *et al*., 2005; Usher *et al*., 2006), ten 10cm soil cores (Bardgett *et al*., 2001) were then collected from each of the four largest habitats per farm and bulked before being stored at 1 – 4 °C and oven dried at 40 °C (Schaffers and Sýkora, 2000). Samples were ground to pass through a 2mm sieve (Ball, 1976; Mapfumo *et al*., 2000). Soil pH was determined on fresh soil using distilled water in a soil:water ratio of 1:2 (Ball, 1976; Western States Laboratory Proficiency Testing Program, 1996); Mapfumo *et al*., 2000). Total Kjeldhal Nitrogen was determined using the Kjeldhal method (Mapfumo *et al*., 2000; Persson *et al*., 2008) and soil organic matter was measured using the standard loss on ignition method (Western States Laboratory Proficiency Testing Program, 1996; Heiri *et al*., 2001), which is considered a reliable predictor of soil organic carbon (SOC) (Ghimire *et al*., 2007; Wright *et al*., 2008). Extractable soil phosphorus was estimated using Morgan's extracting solution (Western States Laboratory Proficiency Testing Program, 1996) and percentage soil moisture content was also measured (Ball, 1976; Rothamsted Research Soil Microbial Biomass Research Group web page, accessed 2009; Snyder *et al*., 2002).

3.3.4 Structural and environmental variables

Vegetation height (cm) was recorded using a sward stick at five points within each relevé and an average calculated. The sward stick is described as the most appropriate method for measuring structural heterogeneity within vegetation (Stewart *et al*., 2001). Altitude (m), slope, aspect, drainage, firmness and percentage cover of exposed rock, litter, bare ground and dung were also recorded per relevé (Dunne, 2000; Dunford, 2001; Hodd, 2007). Total above ground biomass was estimated by clipping all vegetation within an area of 0.25 m^2 inside each 2 m x 2 m relevé to ground level and collecting it in paper bags. Samples were sorted into four major plant growth forms: graminoids, forbs, dwarf shrubs and mosses and oven dried at 80 ° C for 48 hours, then weighed to give an estimate of total above ground biomass (Gordon, 1989; Gardner *et al*., 1997; Holland, 2000), ranging from 1.45 – 395.24 g. ArcGIS 9 (2008) was used to digitise habitat maps for each farm, which allowed the estimation of total area of each habitat per farm, as well as the calculation of variables such as habitat diversity (Shannon-Wiener index).

3.3.5 Invertebrate sampling

Ground beetles, rove beetles (Coleoptera: Carabidae, Staphylinidae) and other beetle families were sampled using pitfall trapping. Pitfall traps are the most widely used method for sampling assemblages of ground-dwelling arthropods (Spence and Niemelä, 1994). Six traps were placed 10m apart along the botanical sampling lines of the four largest habitats in each farm. This maintained a link between the beetle and vegetation data (Dennis *et al*., 1997; Bhriain *et al*., 2002). Traps consisted of plastic cups of 6.5cm diameter and 8cm depth. A 1:3 mixture of ethylene glycol and water was added to the cup, as a preservative, and a few drops of detergent added to the mixture to break the surface tension (Schmidt *et al*., 2006). Covers were made from 10cm x 10cm corrugated plastic, supported about 2cm above the cup using 10cm nails. Covers reduced the risk of traps flooding during heavy rain, as did small holes made near the top of the cups. They also protected the samples from drying out, being consumed by predators or being trampled by livestock (Dennis *et al*., 2001; Cole *et al*., 2006; 2010). Traps were left in situ for three weeks in July and three weeks in October, in order to quantify species active at different periods throughout the year (Dennis *et al*., 1997). Samples were sieved and stored in ethanol for later identification using taxonomic keys (Forsythe, 2000; Luff, 2007). A total of 576 traps were collected, invertebrates collected included 3927 individual carabids, 3909 staphylinids and 1123 other beetles. Carabids were identified to species level, staphylinids to family level and any other beetles were pooled.

Carabid species were split into three groups based on their feeding preferences: generalist predators, specialist predators and phytophagous (plant-eating) species (**Table 3.1**).

3.3.6 Data analysis

3.3.6.1 Carabid abundance, diversity, species richness and evenness

Carabid, staphylinid and other beetle abundance was calculated as the total number of individuals per trap, while species richness was calculated as the total number of species.

Table 3.1 Carabid species and feeding group classification.

Species name	References	Feeding group
Abax parallelepipedus	Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	generalist predator
Agonum fuliginosum	Ribera *et al*. (2001); Cole *et al*. (2002); Haysom *et al*. (2004); Vanbergen *et al*. (2010)	generalist predator
Agonum muelleri	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	generalist predator
Agonum thoreyi	Vanbergen *et al*. (2010)	generalist predator
Anchomenus dorsalis	Harvey *et al*. (2008); Vanbergen *et al*. (2010); Šustek, 2012	generalist predator
Calathus fuscipes	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Carabus clatratus	Huk & Kuhne (1999)	generalist predator
Carabus glabratus	Ribera *et al*. (2001); Cole *et al*. (2002); Vanbergen *et al*. (2010)	generalist predator
Carabus granulatus	Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Carabus problematicus	Cole *et al*. (2002); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	generalist predator
Clivina fossor	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Nebria brevicollis	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	generalist predator
Nebria salina	Cole *et al*. (2002); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Olisthopus rotundatus	Ribera *et al*. (2001); Cole *et al*. (2002); Vanbergen *et al*. (2010)	generalist predator
Poecilus versicolor	Cole *et al*. (2002); Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	generalist predator
Pterostichus diligens	Ribera *et al*. (2001); Cole *et al*. (2002); Haysom *et al*. (2004); Vanbergen *et al*. (2010)	generalist predator
Pterostichus madidus	Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Pterostichus melanarius	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Pterostichus niger	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Pterostichus nigrita	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Pterostichus rhaeticus	Ribera *et al*. (2001); Cole *et al*. (2002); Haysom *et al*. (2004); Vanbergen *et al*. (2010)	generalist predator
Pterostichus strenuus	Ribera *et al*. (2001); Cole *et al*. (2002); Haysom *et al*. (2004); Vanbergen *et al*. (2010)	generalist predator
Pterostichus vernalis	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	generalist predator
Cychrus caraboides	Purtauf *et al*. (2005); Vanbergen *et al*. (2010); Anderson (website accessed Oct 2012)	specialist predator
Leistus fulvibarbis	Haysom *et al*. (2004); Vanbergen *et al*. (2010)	specialist predator
Loricera pilicornis	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	specialist predator
Notiophilus aesthuans	Pfiffner & Luka (2003)	specialist predator
Notiophilus biguttatus	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	specialist predator
Notiophilus germinyi	Harvey *et al*. (2008); Vanbergen *et al*. (2010)	specialist predator
Notiophilus palustris	Cole *et al*. (2002); Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	specialist predator
Trechus obtusus	Ribera *et al*. (2001); Cole *et al*. (2002); Haysom *et al*. (2004); Vanbergen *et al*. (2010)	specialist predator
Amara communis	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	phytophagous
Amara lunicollis	Cole *et al*. (2002); Purtauf *et al*. (2005); Harvey *et al*. (2008); Vanbergen *et al*. (2010)	phytophagous
Amara plebeja	Cole *et al*. (2002); Haysom *et al*. (2004); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	phytophagous
Curtonotus convexiusculus	Anderson (website accessed Oct 2012)	phytophagous
Harpalus latus	Cole *et al*. (2002); Purtauf *et al*. (2005); Vanbergen *et al*. (2010)	phytophagous

Simpson's reciprocal index was adopted as another measure of alpha diversity for each trap:

$$D = 1 / \Sigma P_i^2$$

Where P_i is the relative abundance of species i. Evenness or equitability was calculated by dividing Simpson's reciprocal index by the maximum value Simpson's could take (i.e. total species richness):

$$E_D = D / D_{max}$$

Plant functional diversity was calculated using the Shannon-Wiener index:

$$H' = -\sum_{i=1}^{s} P_i \ln P_i$$

Where s is the number of functional groups, P_i is the proportion of species found in the ith functional group expressed as a proportion of total cover and ln is the natural logarithm. Nine plant functional groups were determined: grasses, forbs, mosses, sedges, shrubs, trees, ferns, lichens and liverworts and rushes. Habitat diversity was also calculated using the Shannon-Wiener index.

3.3.6.2 Carabid consumption rate

Median carabid species lengths (mm) were taken from the length ranges given in Luff (2007). Body lengths were then converted to dry weight biomass (g) using a length-weight relationship defined for the family Carabidae (McLaughlin *et al.*, 2010), $y = 2.82x - 4.92$. A per capita consumption rate was then calculated for each carabid species assuming that consumption (C) is driven by metabolic rate and hence metabolic demand and hence that consumption is proportional to body mass. We based these assumptions on the well-known relationships between metabolism (E) and body mass (M) which scales to the power of 0.75 (Peters, 1983), i.e. $E = M^{0.75} = C$. These species specific per-capita consumption rates were then multiplied by the total number of individuals of each specific species collected in a pitfall trap and a total carabid consumption rate per trap and then per habitat was calculated. The use of body mass to predict consumption rates among predators is now widely accepted (Emmerson and Raffaelli, 2004; Brose *et al*., 2008, Rall *et al*., 2010, Vucic-Pestic *et al*., 2010).

3.3.6.3 Multivariate analysis

Carabid data from each habitat (six pitfall traps) were pooled and data was analysed at the habitat scale. The effects of environmental and management variables on carabid assemblage were explored using the ordination technique, non-metric multidimensional scaling (NMS) in the software package PC-Ord 5 (McCune and Mefford, 1997). NMS provides robust ordinations, resistant to quantitative noise (Minchin, 1987; Enright *et al*., 2005) and is known to be better at recovering complex gradients than some of the more traditional eigenanalysis techniques such as PCA, DCA or CCA (Wilson *et al*., 2006). It is well suited to non-normal data and does not require the transformation of data prior to analysis (Clark, 1993; McCune and Grace, 2002). Carabid samples were arranged in a two or three dimensional space in accordance with the rank order of their ecological similarities. Results were selected on the basis of those NMS plots and solutions which had a minimum number of dimensions and the lowest stress and instability values (McCune and Grace, 2002; Enright *et al*., 2005). A random starting configuration with a maximum of six axes, a stability criterion of 0.0005, 50 permutations with real data, 20 iterations to evaluate stability; a maximum number of iterations of 500; an initial stepdown of 0.2 and 50 randomised permutations for Monte Carlo testing were selected. Sørensen (Bray-Curtis) distance measures were used and all carabid species occurring in less than 5% of the traps in an ordination were excluded (Parr *et al*., 2009). In order to maximise the main component of the variation and the first ordination axis, rotation was applied (Pöyry *et al*., 2004). Relationships between ordination axes and environmental variables were investigated using Spearman’s rank correlations, using R, version 2.14.2 (R Development Core Team, 2012), using the package ‘nlme’ (Pinheiro *et al*., 2012).

3.3.6.4 Univariate analysis

All univariate analyses were performed using R, version 2.14.2 (R Development Core Team, 2012), using the package ‘nlme’ (Pinheiro *et al*., 2012). Carabid data from each habitat (six pitfall traps) was pooled and data was analysed at the habitat scale.

In order to meet the assumptions of normality, the following response variables were transformed: carabid, staphylinid and other beetle abundance and carabid Simpson's diversity were all log transformed, while carabid evenness was arctangent transformed. Soil organic carbon (SOC) was also arctangent transformed. The explanatory variables altitude and plant functional diversity were log transformed, while carabid consumption rate and % scrub were square root transformed. Raw values of the response variable, species richness, and the explanatory variables grazing state, soil moisture, soil pH and vegetation height were analysed.

Variance inflation factors (VIFs) were used to address collinearity issues between explanatory variables (Zuur *et al*., 2009; Zuur *et al*., 2010). All retained variables had a VIF of less than three (Zuur *et al*., 2010). The correlation coefficient threshold of $|r| < 0.7$ between pairwise correlations was also applied (Dormann *et al*., 2012). The independence assumption of linear regression was contravened (clear patterns existed between the response variables and spatial variables month, area and farm), therefore linear mixed effects models (LMMs) with residual maximum likelihood estimation (REML) were implemented. Forward stepwise selection procedures were used to select each model based on the lowest Akaike's information criterion (AIC). Grazing state (farm level: 3 categories, balanced), grazing state (habitat level: 5 categories, unbalanced), stocking rate of sheep (4 categories, unbalanced), altitude, carabid consumption rate, plant functional diversity, soil moisture and pH, % signs of grazing, % shrubs and % scrub were analysed as fixed effects. Farm (12 levels) was nested within area (4 levels), which was nested within month (2 levels), and therefore all three factors were treated as random effects.

The minimal adequate model was selected using model simplification. In most incidences this was a *random intercept model*, however, occasionally the *random slope model* provided a more accurate fit to the data. Model validation involved checking for homogeneity using plots of standardised residuals versus fitted values, as well as standardised residuals versus the explanatory variables used in each model. QQ-plots and histograms of the model residuals were used to assess normality, in conjunction with the Shapiro-Wilk test. REML was used to estimate the random effects terms and Maximum Likelihood (ML) was used to quantify the fixed effects. The likelihood ratio test systematically compared each interaction with the whole model to allow the retention of terms with significant explanatory power (Zuur *et al*., 2009).

Only parameter estimates and standard errors are reported for the LMMs, as the associated p-values can be unreliable (Baayen *et al.*, 2008). However p-values have been reported in relation to overall effects of explanatory variables, using the anova function. When using sequential sum of squares, the order of variables in the model is important (Zuur *et al.*, 2009; Hector *et al.*, 2010), therefore Type III Sum of Squares were adopted. The use of Type III Sum of Squares whilst controversial (Hector *et al.*, 2010), was considered justified on this occasion.

3.4 Results

3.4.1 Carabid assemblage

NMS ordination explained 58.8% of the variation in carabid species abundance. Axis 1 accounted for 21.6%, Axis 2, 15.5% and Axis 3, 21.7% of the variation (**Appendix A S3.1**). Axis 1 clearly reflected a gradient in grazing management, with higher percentages of dung, signs of grazing and stocking rates of sheep at one end and taller vegetation and a greater percentage of litter at the other end. *Carabus clatratus*, *C. problematicus* and *Nebria salina* were more abundant at the more intensively grazed end, while *Abax parallelepipidus*, *Carabus granulatus* and *Pterostichus niger* were found in greater numbers under lower levels of grazing. Axis 2 was significantly correlated with the percentage of traditional ewes on a farm, suggesting another gradient of grazing management. *Pterostichus niger*, *P. nigrita*, *Agonum fuliginosum* and *A. thoreyi* were all negatively affected by this axis. Axis 3 was significantly correlated with soil moisture and pH and inversely correlated with altitude, soil nitrogen and plant functional diversity. *Nebria brevicollis*, *Pterostichus madidus*, *P. strenuus*, *P. vernalis*, *P. melanarius*, *Poecilus versicolor*, *Agonum muelleri* and *Calathus fuscipes* were all positively associated with this axis, suggesting their affinity for the lowlands, while *Pterostichus diligens* and *P. rhaeticus* were negatively affected, being more abundant in the uplands.

3.4.2 Functional feeding groups

3.4.2.1 Generalist predators

The NMS ordination explained 57.8% of the variation in generalist predator abundance. Axis 1 accounted for 21.8% of the variation, Axis 2, 12.3 and Axis 3, 23.8% (**S3.2**). Axis 1 was significantly correlated with soil moisture and pH and inversely correlated with altitude, soil nitrogen and plant functional diversity. *Pterostichus madidus*, *P. niger*, *P. strenuus*, *P. vernalis*, *P. melanarius*, *Poecilus versicolor*, *Agonum muelleri*, *A. fuliginosum* and *Calathus fuscipes* were all positively associated with this axis, suggesting their affinity for the lowlands, while *Pterostichus diligens*, *P. rhaeticus* and *Carabus clatratus* were negatively affected, being more abundant in the uplands. Axis 2 was significantly correlated with % shrubs in a habitat, another potential grazing management axis. *Carabus problematicus* and *Nebria salina* were both positively associated with the % shrubs, while *Pterostichus nigrita*, *P. melanarius*, *Agonum muelleri* and *Carabus granulatus* were negatively affected, preferring areas of low shrub cover. Axis 3 again appeared to follow a gradient of grazing management, with high levels of grazing, % dung and sheep stocking rate at one end of the scale and tall vegetation and a high percentage of litter at the other. *Nebria brevicollis*, *N. salina* and *Calathus fuscipes* were all positively associated with this axis, while *Abax parallelepipidus* and *Carabus granulatus* were negatively affected by increased grazing intensity.

3.4.2.2 Specialist predators

The NMS ordination explained 76.4% of the variation in specialist predator abundance. Axis 1 accounted for 31.7% and Axis 2, 44.7% (**S3.3**). Axis 1 was significantly correlated with the percentage of traditional ewes on a farm. *Notiophilus germinyi* was more abundant when the percentage of traditional ewes was high, while *Notiophilus palustris* preferred a lower percentage of traditional ewes, perhaps indicating a preference for higher levels of grazing. Axis 2 was significantly correlated with altitude and inversely correlated with vegetation height. *Trechus obtusus* appeared to favour higher altitudes, while *Cychrus caraboides* preferred taller vegetation.

3.4.2.3 Phytophagous species

NMS ordination explained 83.5% of the variation in phytophagous carabid abundance. Axis 1 accounted for 23.9%, Axis 2, 29.2% and Axis 3, 30.4% of the variation (**S3.4**). Axis 1 was significantly correlated with soil pH and the % forbs in a habitat and inversely correlated with % shrubs. *Amara plebeja* appears to have an affinity for areas with higher soil pH (lowlands) and lower shrub cover (higher level of grazing). Axis 2 was significantly correlated with % scrub on a farm and inversely correlated with altitude. *Amara lunicollis* favoured lowland habitats with higher scrub cover (lower level of grazing). Axis 3 was significantly correlated with signs of grazing and % dung and negatively influenced by vegetation height and scrub cover. *Amara lunicollis* again favoured areas of high vegetation height and scrub cover.

3.4.3 Univariate analysis

Preliminary observations indicated that phytophagous carabid abundance was greater in the lowlands, where soil pH was high, nitrogen levels low and percentage of grass high. However, as only five phytophagous species were collected, comprising only 12 individuals, statistical analysis was not possible. There were ten species of specialist predator but 65 individuals so it was possible to analyse specialist predator abundance. Altitude and vegetation height had a significant effect on specialist predator abundance ($F_{1,67}$: 7.448, p = 0.008) (**Table 3.2**), with more individuals detected in the uplands in shorter vegetation. Stocking rate of sheep was also influential ($F_{3,13}$: 4.544, p = 0.022). Greater specialist predator abundance was detected under stocking rate 2 (0.21 – 0.4 LU/ha) than stocking rate 1 (0 – 0.2 LU/ha) (estimate 0.176 ± se 0.059), stocking rate 3 (0.41 – 0.6 LU/ha) (estimate 0.152 ± se 0.062) or stocking rate 4 (0.61 – 0.8 LU/ha) (estimate 0.231 ± se 0.068). There was a significant effect of grazing state (habitat level) and altitude on generalist predator abundance ($F_{4,63}$: 3.009, p = 0.025) (**Table 3.2**) and species richness ($F_{4,63}$: 2.962, p = 0.026) (**Table 3.2**), with generalist predator abundance and species richness increasing with altitude under light-moderate and moderate-heavy grazing levels and decreasing with altitude under light, moderate and heavily grazed states. There was also a significant effect of grazing state (farm level), altitude and plant functional diversity on generalist predator species richness ($F_{2,63}$: 3.701, p = 0.03) (**Table 3.2**), with altitude and plant functional diversity having a positive effect on generalist predator species richness under a light or lightly-moderately grazed state and a negative effect under a heavily grazed state. There were 27 species of generalist predator analysed, consisting of 3858 individuals.

Table 3.2 Best fit models for functional carabid feeding groups, carabid, staphylinid and other beetle abundance and diversity and soil organic carbon (SOC) (* indicates interaction between variables).

Response variable	Fixed effects			Random effects		
log$_{10}$(specialist predator abundance)	sheep stocking rate +	log$_{10}$(altitude) *	vegetation height	1 | month /	site /	farm
log$_{10}$(generalist predator abundance)	grazing state (habitat level) *	log$_{10}$(altitude)		1 | month /	site /	farm
generalist predator species richness	grazing state (habitat level) *	log$_{10}$(altitude)		1 | month /	site /	farm
generalist predator species richness	grazing state (farm level) *	log$_{10}$(altitude) *	log$_{10}$(plant functional diversity)	1 | month /	site /	farm
log$_{10}$(carabid abundance + 1)	grazing state (habitat level) *	log$_{10}$(altitude)		1 | month /	site /	farm
log$_{10}$(carabid abundance + 1)	grazing state (farm level) +	log$_{10}$(altitude)		1 | month /	site /	farm
log$_{10}$(carabid abundance + 1)	grazing state (farm level) *	log$_{10}$(altitude) *	log$_{10}$(plant functional diversity)	1 | month /	site /	farm
atan(evenness)	grazing state (habitat level) +	log$_{10}$(altitude)		1 | month /	site /	farm
atan(evenness)	grazing state (farm level) +	log$_{10}$(altitude)		1 | month /	site /	farm
species richness	grazing state (habitat level) *	log$_{10}$(altitude)		1 | month /	site /	farm
species richness	grazing state (farmlevel) +	log$_{10}$(altitude)		1 | month /	site /	farm
log$_{10}$(staphylinid abundance + 1)	grazing state (habitat level) *	log$_{10}$(altitude)		(altitude -1) | month /	site /	farm
log$_{10}$(staphylinid abundance + 1)	grazing state (farm level) +	log$_{10}$(altitude)		(altitude -1) | month /	site /	farm
log$_{10}$(staphylinid abundance + 1)	grazing state (farm level) *	log$_{10}$(altitude) *	soil moisture	(altitude -1) | month /	site /	farm
log$_{10}$(other beetle abundance + 1)	grazing state (habitat level) *	log$_{10}$(altitude)		(altitude -1) | month /	site /	farm
log$_{10}$(other beetle abundance + 1)	grazing state (farm level) +	log$_{10}$(altitude)		(altitude -1) | month /	site /	farm
log$_{10}$(other beetle abundance + 1)	sheep stocking rate *	log$_{10}$(altitude) *	soil pH	(altitude -1) | month /	site /	farm
atan(SOC)	log$_{10}$(abundance + 1) *	grazing state (farm level) *	soil moisture	1 | month /	site /	farm
atan(SOC)	log$_{10}$(abundance + 1) *	grazing state (habitat level)		1 | month /	site /	farm
atan(SOC)	log$_{10}$(abundance + 1) *	sheep stocking rate *	soil moisture	1 | month /	site /	farm
atan(SOC)	species richness *	grazing state (farm level) *	soil moisture	1 | month /	site /	farm
atan(SOC)	species richness *	grazing state (habitat level)		1 | month /	site /	farm
atan(SOC)	species richness *	sheep stocking rate		1 | month /	site /	farm
atan(SOC)	atan(evenness) *	grazing state (habitat level)		1 | month /	site /	farm
atan(SOC)	log$_{10}$(other beetle abundance + 1) *	grazing state (farm level) *	soil moisture	1 | month /	site /	farm
atan(SOC)	sqrt(consumption rate) *	grazing state (farm level) *	sqrt($_{\%}$ scrub)	1 | month /	site /	farm

3.4.4 Notable and other locally distributed species

Notable species have restricted distributions and are classified as nationally scarce in Britain (Hyman and Parsons, 1992; Vanbergen *et al.*, 2005). Five carabid species collected in the present study deserve a special mention. One individual of the scarce species *Cymindis vaporariorum* (Notable B category) was discovered on moderately grazed montane heath at 563m and one individual of the very scarce species *Notiophilus aesthuans* (Notable B category) was found on moderately grazed upland blanket bog at 464m. As far as the authors are aware, this is a considerable expansion of the range of both *Cymindis vaporariorum* and *Notiophilus aesthuans* (Alexander, 1994; Stephen McCormack, pers. comm.). The large carabid *Carabus clatratus* (Notable A category), which is in decline in Western Europe and is very locally distributed, was found in many of the upland and lowland blanket bogs of varying grazing intensity in the present study. There were also two species which are not classified as notable but are nonetheless uncommon. Two individuals of the species *Curtonotus convexiusculus* [in Ireland this species is known to only be abundant in Co. Waterford (Luff, 2007)], were found on improved grassland on a heavily grazed site, relatively near the coast, at an altitude of 115m and nine individuals of the species *Carabus glabratus* were discovered on a lightly-moderately grazed upland blanket bog above 480m.

3.4.5 Carabid abundance and species richness

3927 individual carabids were analysed (42 species). A significant interaction between grazing state and altitude was found for carabid abundance but only when grazing state was classified at the smaller level of habitat, as opposed to the whole farm level ($F_{4,63}$: 2.83, p = 0.032) (**Table 3.2**, **Fig. 3.2**). The carabid abundance of state 1 (lightly grazed), state 3 (moderately grazed) and state 5 (heavily grazed) were all negatively influenced by altitude, while state 2 (lightly-moderately grazed) and state 4 (moderately-heavily grazed) both displayed a positive relationship with altitude. State 4 exhibited significantly greater carabid abundance than state 1 (estimate 3.268 ± se 1.514), state 3 (estimate 3.551 ± se 1.51) or state 5 (estimate 4.225 ± se 1.599). State 2 also displayed greater abundance than state 5 (estimate 1.401 ± se 0.675). Grazing states (measured at the habitat level) appear to intersect at an elevation of around 200m, with low carabid abundance, particularly in state 4, below 100m.

Although there was no significant interaction between grazing state and altitude for carabid abundance at the farm level, the main effects of grazing state ($F_{2,14}$: 4.71, $p = 0.027$) (**Table 3.2**), and altitude ($F_{1,71}$: 7.634, $p = 0.007$) (**Table 3.2**), played a significant role in determining carabid abundance. Grazing state had a positive effect on carabid abundance, with both state 2 (estimate 0.283 ± se 0.11) and state 3 (estimate 0.297 ± se 0.107) exhibiting greater abundance than state 1, while altitude had a negative effect. However, when plant functional diversity was included as a main effect, a grazing state and altitude interaction was found to have a significant effect on carabid abundance at the farm level ($F_{2,63}$: 3.199, $p = 0.048$) (**Table 3.2**).

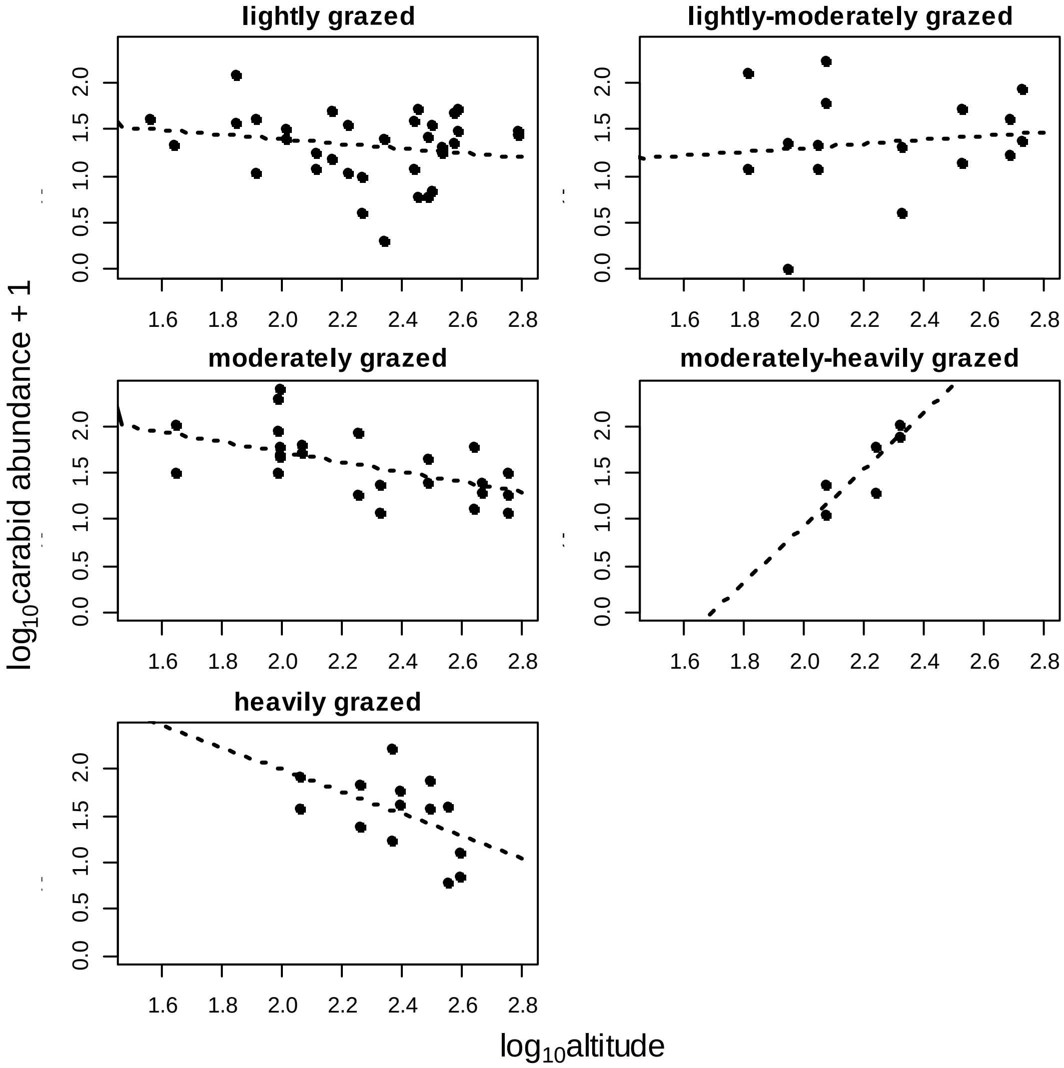

Fig. 3.2 Effect of grazing state (habitat level classification) and $\log_{10}$ altitude on $\log_{10}$ (carabid abundance + 1). Moderately-heavily grazed habitats exhibited significantly greater upland carabid abundance than other grazing states, perhaps due to indirect vegetation effects or the presence of an assemblage of specialist carabid species. However, increased replication may address this.

There was no effect of grazing state or altitude on carabid Simpson's diversity at either the farm or habitat level. There was, however, a significantly positive effect of altitude on carabid evenness at both the habitat ($F_{1,67}$: 4.486, $p = 0.038$) and farm ($F_{1,71}$: 6.96, $p = 0.01$) levels but no influence of grazing state (**Table 3.2**).

Grazing state exhibited a hump shaped relationship with carabid species richness at the habitat level ($F_{4,63}$: 3.158, $p = 0.02$) (**Table 3.2**, **Fig. 3.3**) and the farm level ($F_{2,14}$: 7.968, $p = 0.005$) (**Table 3.2**, **Fig. 3.4**), with moderately grazed state 3 containing significantly more carabid species than either lightly grazed state 1 (estimate 10.888 ± se 4.317) or lightly-moderately grazed state 2 (estimate 12.285 ± se 5.101) at the habitat level and lightly-moderately grazed state 2 (estimate 0.405 ± se 0.646) and state 3 (estimate 1.991 ± se 0.624) containing significantly greater carabid species richness than state 1 at the farm level. There was also a negative effect of altitude at the farm level ($F_{1,71}$: 8.881, $p = 0.004$) (**Table 3.2, Fig. 3.5**).

A grazing state – altitude interaction at the habitat level played a significant role in determining staphylinid abundance ($F_{4,63}$: 2.814, $p = 0.033$) (**Table 3.2**). Staphylinid abundance was greater in state 4 than state 1 (estimate 4.661 ± se 1.859), state 2 (estimate 3.826 ± se 1.874), state 3 (estimate 4.842 ± se 1.858) or state 5 (estimate 4.182 ± se 1.962). There was also significantly greater staphylinid abundance in state 2 than in state 3 (estimate 1.016 ± se 0.467). Staphylinid abundance presented a similar pattern to that of carabid abundance, in that it too declined with altitude under grazing states 1, 3 and 5. There was a slightly positive effect of altitude on staphylinid abundance in grazing state 2, however it was grazing state 4 which again showed a highly significant increase in staphylinid abundance with altitude. There was, however, a negative effect of altitude on staphylinid abundance ($F_{1,71}$: 4.939, $p = 0.029$) at the farm level (**Table 3.2**). A three-way interaction between grazing state (farm level), altitude and soil moisture was also found to have a significant effect on staphylinid abundance ($F_{2,63}$: 4.088, $p = 0.021$) (**Table 3.2**).

There was also a significant interaction between grazing state and altitude on other beetle abundance at the habitat level ($F_{4,63}$: 2.993, p = 0.025). (**Table 3.2**). Other beetle abundance was greater in state 4 than state 1 (estimate 6.087 ± se 1.962), state 2 (estimate 5.52 ± se 1.979), state 3 (estimate 6.123 ± se 1.963) or state 5 (estimate 6.588 ± se 2.09). Other beetle abundance revealed a similar pattern to that of carabid and staphylinid abundance, also declining with altitude under grazing states 1, 3 and 5 but also under grazing state 2, while again, grazing state 4 displayed a highly significant increase in other beetle abundance with altitude. Altitude ($F_{1,71}$: 16.946, p = 0.0001) and grazing state ($F_{2,14}$: 5.663, p = 0.016) both played a significant role in explaining other beetle abundance at the farm level, with state 2 exhibiting greater abundance than state 1 (estimate 0.359 ± se 0.135) or state 3 (estimate 0.405 ± se 0.129) (**Table 3.2**).

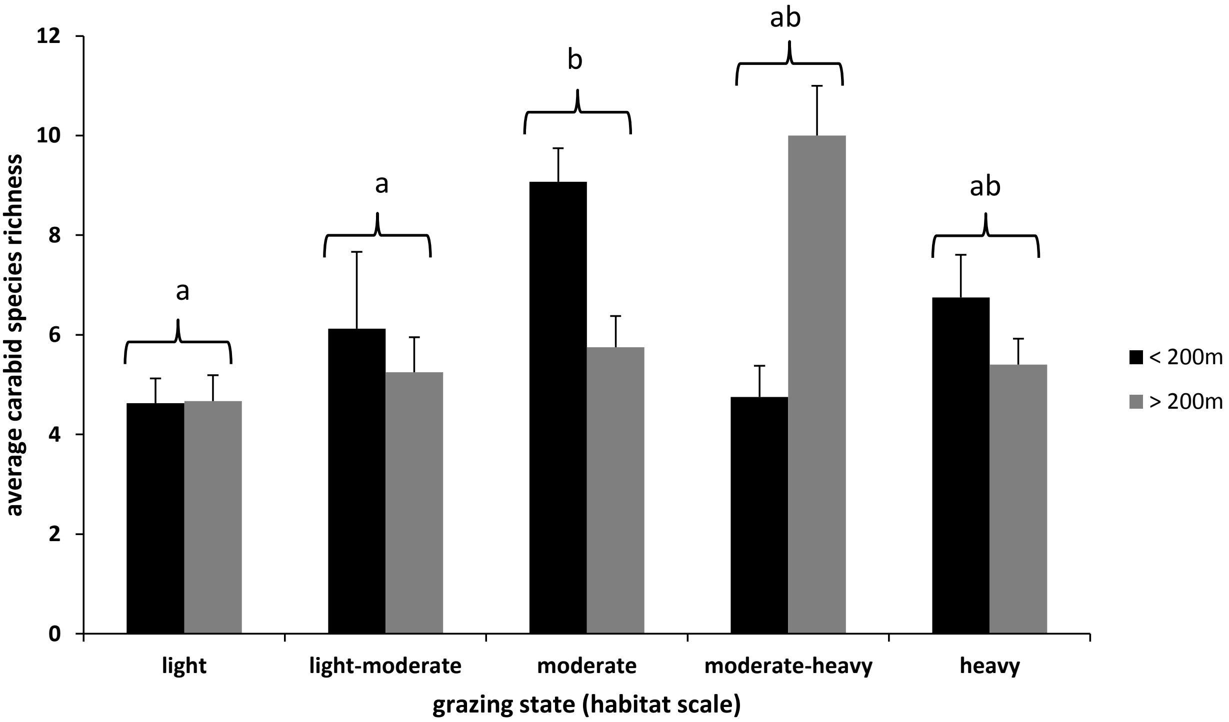

Fig. 3.3 Influence of grazing state (habitat level classification) on carabid species richness in the lowlands (< 200m) and the uplands (> 200m).

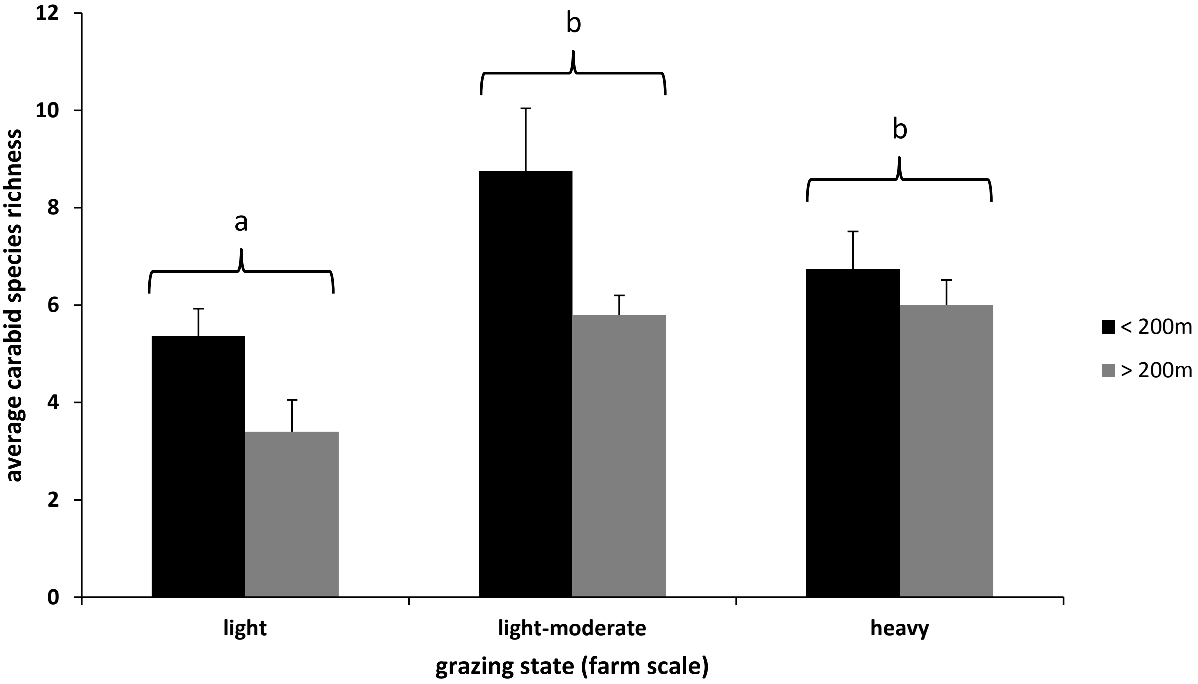

Fig. 3.4 Influence of grazing state (farm level classification) on carabid species richness in the lowlands (< 200m) and the uplands (> 200m).

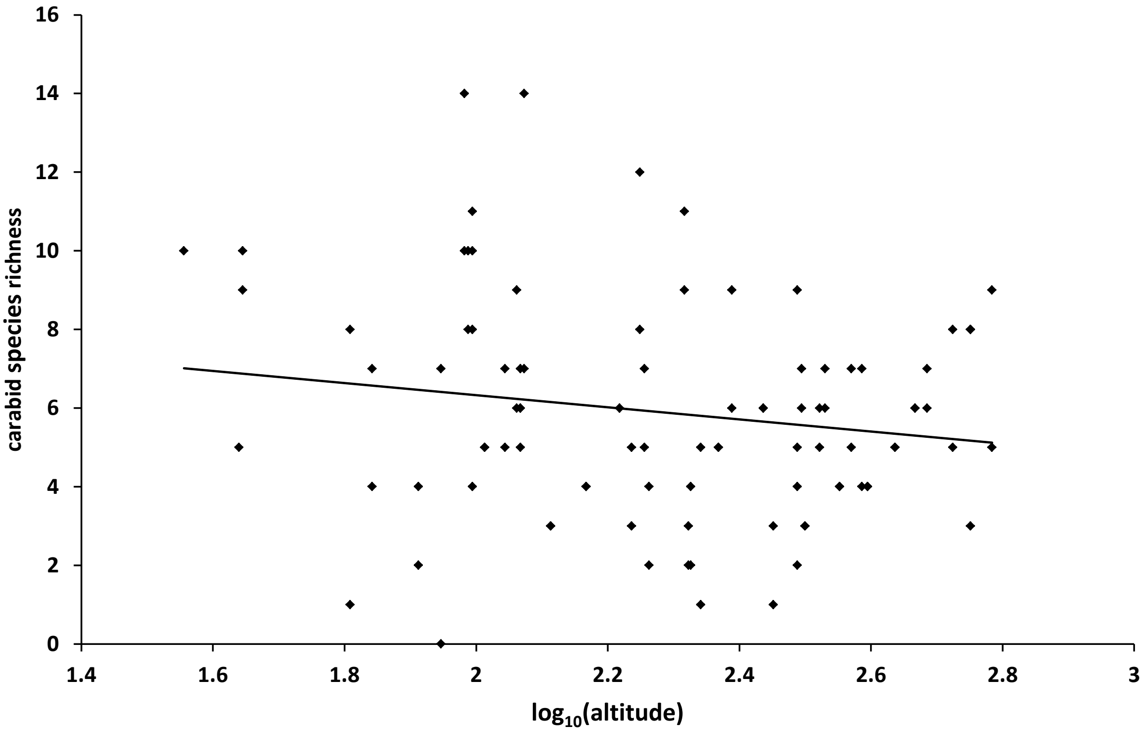

Fig. 3.5 Effect of log$_{10}$ altitude on carabid species richness.

3.4.6 Effect of carabid abundance and species richness on the ecosystem service soil organic carbon

The ecosystem service measure of soil organic carbon (SOC) was significantly influenced, at the farm level, by a three-way interaction between carabid abundance, grazing state and soil moisture ($F_{2,63}$: 5.069, $p = 0.009$) (**Table 3.2**) and also by a three-way interaction between carabid species richness, grazing state and soil moisture ($F_{2,63}$: 5.236, $p = 0.008$) (**Table 3.2**). A three-way interaction between other beetle abundance, grazing state and soil moisture also had a significant effect on SOC ($F_{2,63}$: 17.038, $p < 0.0001$) (**Table 3.2**). At the habitat level, an interaction between carabid abundance and grazing state had a significant effect on SOC ($F_{4,63}$: 4.648, $p = 0.002$) (**Table 3.2**, **Fig. 3.6**), as did the interaction between carabid species richness and grazing state ($F_{4,63}$: 7.745, $p < 0.0001$) (**Table 3.2**), and carabid evenness and grazing state ($F_{4,63}$: 3.339, $p = 0.015$) (**Table 3.2**). **Fig. 3.6** shows that there was a negative effect of carabid abundance on SOC in all grazing states at the habitat level. However, the relationship between SOC and carabid abundance in state 4 is far steeper than that of the other states. SOC levels were significantly lower in state 4 than in state 1 (estimate -0.168 ± se 0.041), state 2 (estimate -0.14 ± se 0.041), state 3 (estimate -0.153 ± se 0.042) or state 5 (estimate -0.178 ± se 0.045).

The stocking rate of sheep on the farms was also found to influence SOC. The three-way interaction between carabid abundance, stocking rate of sheep and soil moisture ($F_{3,60}$: 2.991, $p = 0.038$) (**Table 3.2**), and the interaction between carabid species richness and stocking rate of sheep ($F_{3,68}$: 10.091, $p < 0.0001$) (**Table 3.2**), both played a significant role in determining SOC levels.

3.4.7 Effect of carabid consumption on ecosystem services

A three-way interaction between total carabid consumption rate, grazing state and % scrub at the farm level, was found to have a significant effect on SOC ($F_{2,66}$: 3.685, $p = 0.03$) (**Table 3.2**, **Fig. 3.7** & **Fig. 3.8**). To help disentangle the three-way interaction, **Fig. 3.7** displays the effects of carabid consumption rate alone on SOC. There was no significant interaction between carabid consumption rate and grazing state on SOC, at the farm level. However, grazing state 1 was significantly different to state 2 (estimate 0.042 ± se 0.019), with SOC increasing with carabid consumption rates in states 2 and 5 and decreasing in state 1. There was no significant interaction effect of % scrub and grazing state on SOC at the farm level either (**Fig. 3.8**). However, in states 1 and 2, SOC declined as % scrub increased, while SOC rose along with an increase in % scrub in the heavily grazed state 5.

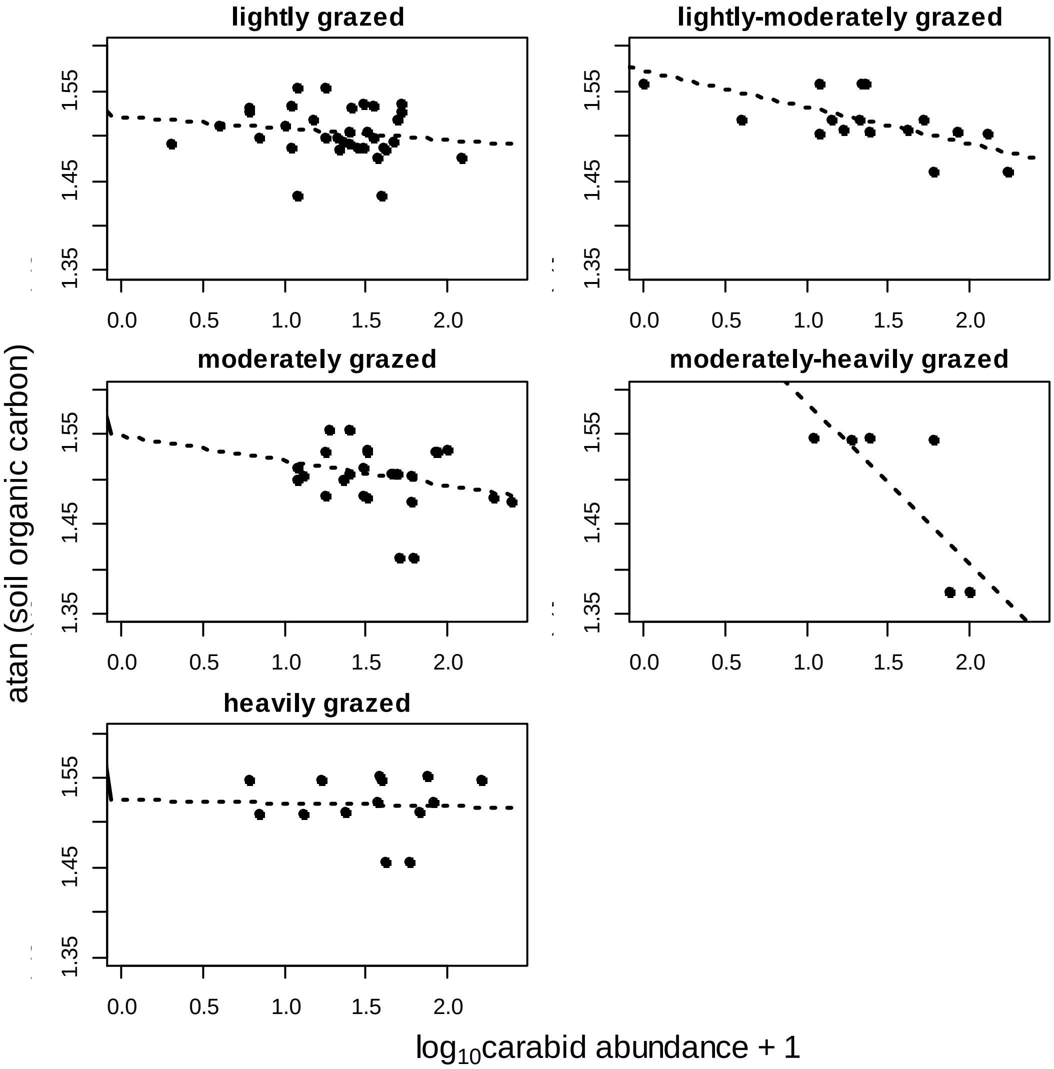

Fig. 3.6 Influence of $\log_{10}$ (carabid abundance + 1) and grazing state (habitat level classification) on soil organic carbon (SOC).

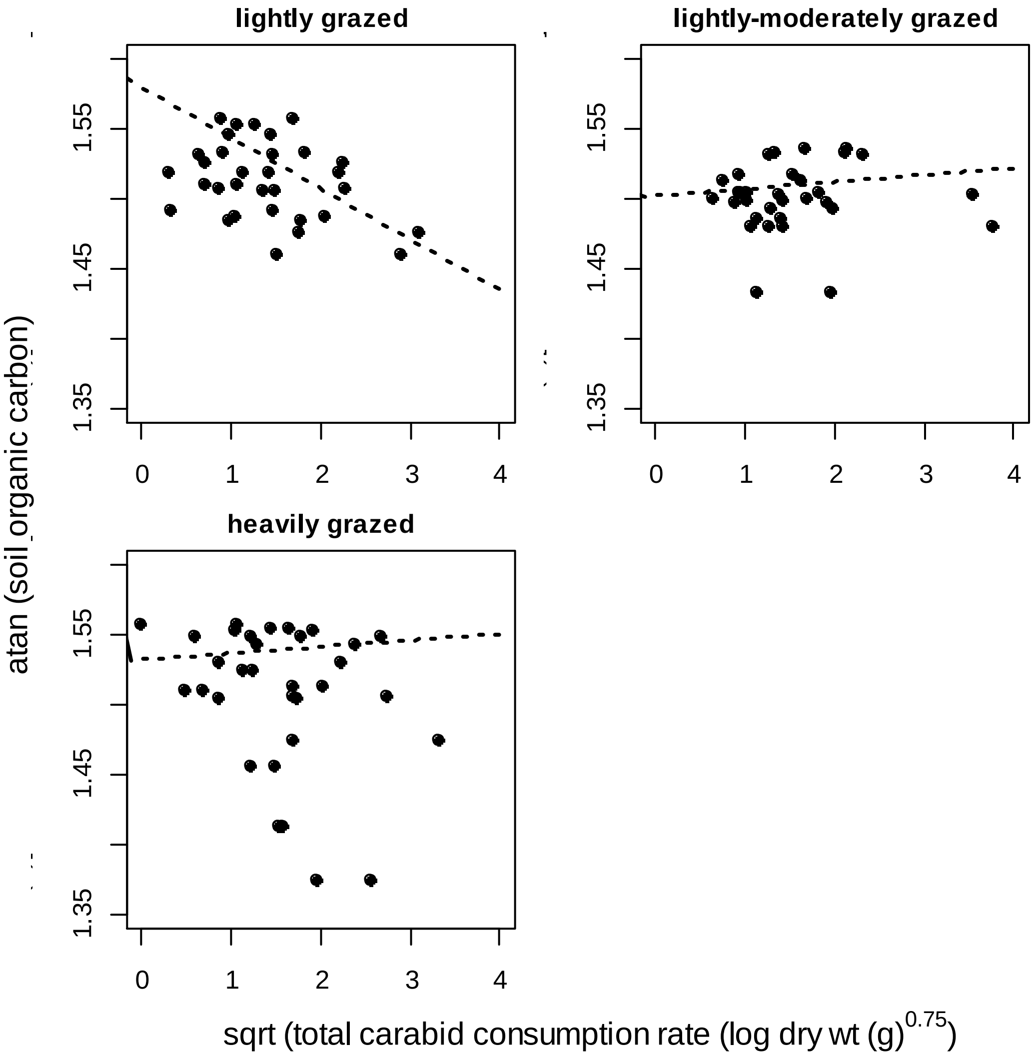

Fig. 3.7 Effect of sqrt (carabid consumption rate) on % soil organic carbon (SOC) across grazing state (farm level classification).

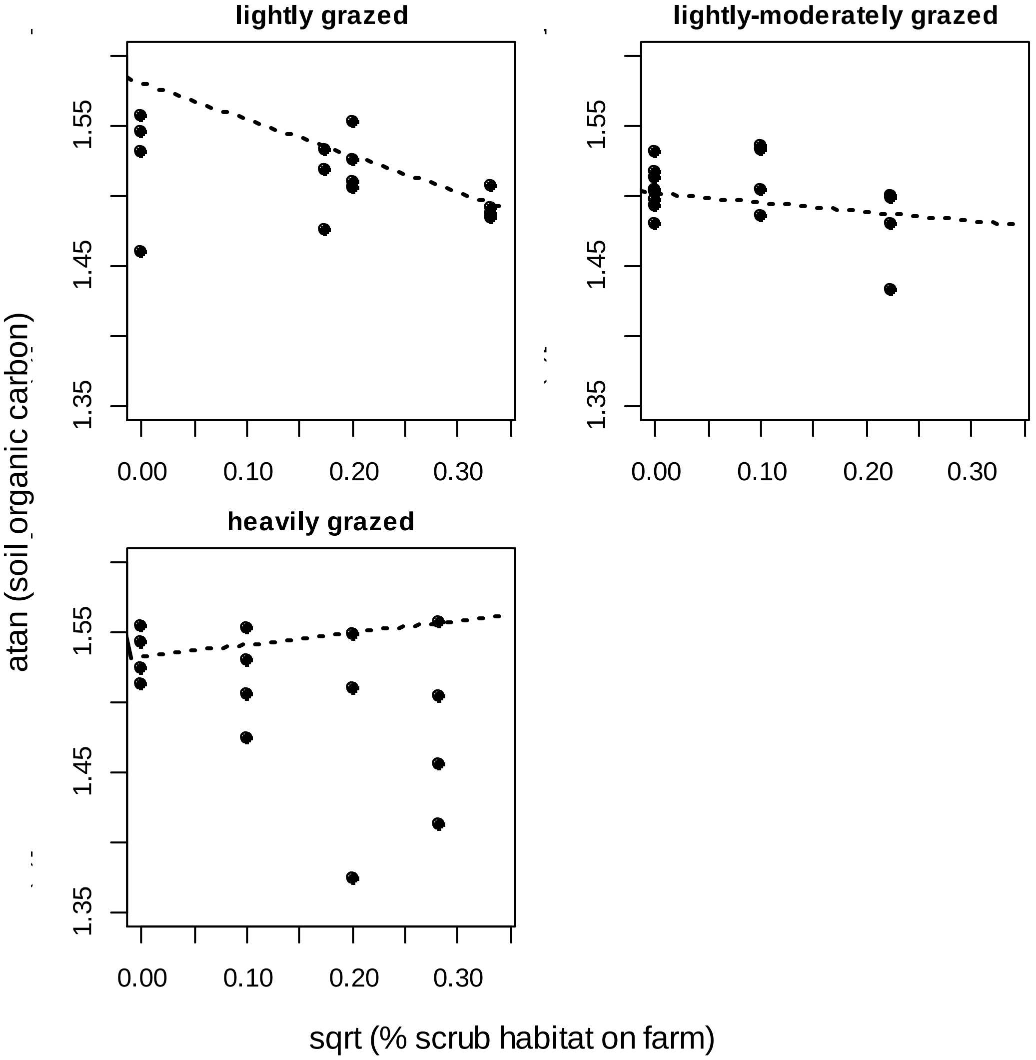

Fig. 3.8 Effect of sqrt (% scrub on farm) on % soil organic carbon (SOC) across grazing state (farm level classification).

3.5 Discussion

Grazing management can affect carabids at both the species and assemblage level (Luff and Rushton, 1989; Dennis *et al*., 1997; Cole *et al*., 2006). Different species may favour particular habitat types, however, this is often dependent upon geographical location (Cole *et al*., 2006). Diversity indices have been used in many carabid studies (Butterfield and Coulson, 1983; Luff and Rushton, 1989; Fournier and Loreau, 2001; Woodcock *et al*., 2007), however they often, as in the present study, fail to evaluate changes in ground beetle communities (Dritschilo and Erwin, 1982), suggesting that the use of ecological or functional groupings may provide more information (Vanbergen *et al*., 2005; Cole *et al*., 2006). This then allows the 'value' of species to be considered, perhaps by recording their rarity status at a local, national and international level (Downie *et al*., 1998).

3.5.1 Carabid assemblage

Carabid trophic groups are known to respond differently to agricultural intensification (Purtauf *et al*., 2005; Schweiger *et al*., 2005; Vanbergen *et al*., 2010). By analysing generalist and specialist predators and phytophagous carabids separately, the incidence of one trophic group masking any management or environmental effects of another was removed (Lövei, 2008). The effects of altitude on generalist predator abundance and species richness was dependent upon grazing state and in fact, this effect became more pronounced when feeding groups were analysed separately, suggesting clearly defined ecosystem roles. This study found that the majority of generalist predators and phytophages were more abundant in the lowlands, while specialist predators were more abundant in the uplands. A high percentage of grass cover was important for phytophages, while preferred grazing intensity was species dependent. Specialist predators appeared to have an affinity for shorter vegetation, while generalist abundance and species richness was dependent upon the interaction between altitude and grazing state. Plant functional diversity was also clearly important in explaining effects of generalist species richness at the farm level.

Pterostichus nigrita, *P. melanarius*, *Agonum muelleri* and *Carabus granulatus* were found in areas of low shrub cover. *Pterostichus melanarius*, *P. niger*, *Poecilus versicolor*, *Agonum muelleri*, *A. fuliginosum*, *Calathus fuscipes*, *P. strenuous* and *P. vernalis* are widespread species, found particularly on damp grassland (Luff *et al*., 1989; Rushton *et al*., 1991; Luff, 1998; Luff, 2007), where *P. melanarius* prefers open habitats (Butterfield and Coulson, 1983) and *P. vernalis* has a preference for undergrazed sites containing a high percentage of litter (Luff, 1998). These species were also inversely correlated with plant functional diversity, perhaps reflecting the fact that the majority of damp lowland grasslands sampled were intensively managed improved grassland, which tends to have an impoverished flora (Davies, 2002), consisting of low species richness and poor structural diversity in comparison to extensively managed grassland (Marriott *et al*., 2004). *Pterostichus niger*, *P. nigrita*, *Agonum fuliginosum* and *A. thoreyi* favoured farms with a low percentage of traditional ewes, perhaps indicating a preference for more commercial grazing management. Although Holmes *et al*. (1993) found that *Agonum fuliginosum* and *A. thoreyi* preferred ungrazed areas. However, *Pterostichus niger* had a preference for lower levels of grazing, so this axis may be explained by a factor other than simply grazing intensity, such as soil moisture, as it is a species typical of wet peatland (Butterfield and Coulson, 1983). *Carabus clatratus*, *C. problematicus*, *Pterostichus melanarius*, *Nebria brevicollis*, *N. salina* and *Calathus fuscipes* were abundant in heavily grazed areas, and *Pterostichus melanarius* and *Nebria brevicollis* are known to occur more frequently in intensively grazed sites (Dennis *et al*., 2004; Vanbergen *et al*., 2005). It appears that *Nebria salina* also favours high shrub cover (McFerran *et al*., 1994), so may be a habitat generalist, or influenced to a greater extent by another factor. While *Abax parallelepipidus*, *Carabus granulatus* and *Pterostichus niger* were more common under less intensive grazing. This finding is supported by the fact that *Abax parallelepipidus* is a poor disperser and therefore unlikely to be able to adapt to a high level of disturbance, although *Pterostichus niger* is known to have good dispersal power (Lövei and Sunderland, 1996). The finding of *Carabus clatratus* and *C. problematicus* under a high level of grazing is surprising, as studies have shown that large carabids of the *Carabus* genus have a strong affinity for heathland (McFerran *et al*., 1994) and are adversely affected by intensive management practices (Luff and Rushton, 1989; Rushton *et al*., 1989; Blake, 1996; Ribera *et al*., 2001; Cole *et al*., 2002, 2005), particularly those of cattle grazing (Butterfield *et al*., 1995). Large carabids are known to predate large plant bugs, which are abundant in structurally diverse unfertilised grassland (Curry, 1994; Lang *et al*., 1999). Indeed the large locally distributed carabid, *Carabus clatratus*, is known to favour heavily vegetated areas (Hyman and Parsons, 1992; McFerran *et al*., 1995). However, some have suggested that small arthropods are actually more sensitive than large beetles to intensive grazing in the uplands (Dennis *et al*., 1998), although others have shown that the majority of carabids caught in intensively managed sites do tend to be small, highly mobile species, capable of flight (Luff and Rushton, 1989; Dennis, 2003). Nevertheless, Williams and Gormally (2010) noted that *C. clatratus*, was also found in high numbers on bare or eroded ground, suggesting that these areas were used as basking habitats (owing to their high dependence on ground temperature), as opposed to a requirement for shorter vegetation. This may explain why this species was found to be more common on heavily grazed sites in the present study. Sites subject to higher levels of grazing provide more favourable soil temperatures (due to decreased shading). Shorter more open vegetation provides ideal foraging conditions for small diurnal carabids, which use visual cues to catch their prey (Cole *et al*., 2012b). Conversely, tall vegetation and a high percentage of litter, in lightly grazed areas, delivers increased prey abundance (particularly that of snails and worms, which are sensitive to desiccation in short vegetation) and a greater availability of hibernation sites for large carabids (Brose, 2003b; Cole *et al*., 2005; Lenoir and Lennartsson, 2010), which tend to hunt nocturnally using tactile cues (Cole *et al*., 2012b).

In the present study all carabids, as well as generalist predators on their own (comprising over 64% of the species pool), were found to be more common at low altitudes with high levels of soil moisture and a high pH, suggesting a preference for damp lowland grassland. In fact soil moisture and site wetness are crucial in determining the selection of microhabitats by carabids, which is often dependent upon the conditions required for larval and immature adult growth (Harde, 1984; Gardner, 1991; Rushton *et al*., 1991; Lövei and Sunderland, 1996; Huk and Kuhne, 1999; Bhriain *et al*., 2002; Dennis, 2003). Predatory beetle larvae are also influenced by management practices, favouring intensively managed grassland (Cole *et al*., 2012a). Carabids with larvae that can overwinter in the soil (where it is warmer) are at an advantage in cooler upland habitats (Sota, 1996; Cole *et al*., 2005).

Analysis of the generalist predators only revealed that beetles of the *Carabus* genus were *not* abundant in heavily grazed areas, as expected. This clearly shows the value of using functional groups in assemblage analysis. *C. clatratus* and *C. problematicus* were found to frequent areas of high shrub cover with high nitrogen levels. Cole *et al*. (2002) also noted that *Carabus* species were more abundant in heather moorland, where they had a plentiful supply of food. These species are known to reside in heath and long grassland, often in the uplands (Luff, 1998; McCormack *et al*., 2006). The large body size, long life cycles (*K*-selected species, Begon *et al*., 1996), and flightless nature of *Carabus* spp, have been suggested as factors involved in preventing their adaptation to the highly fluctuating conditions of more intensively grazed sites (Cole *et al*., 2002; 2006). However, *Carabus problematicus* has a range of over 500m (Rushton *et al*., 1991), and has been found to hunt in short grass, while seeking refuge in longer grass (Butterfield *et al*., 1995), highlighting the fact that the use of vegetation structure by carabids is highly dependent upon their functional requirements. Extensively grazed systems provide a more stable microclimate through the buffering of environmental fluctuations through a combination of tall grass and a reduction in livestock trampling, defecating and grazing (Dennis *et al*., 1998; Cole *et al*., 2010). Sward height can actually alter thermal conditions at rates above those predicted by climate change (Suggitt *et al*., 2011). A tall heterogeneous sward structure has been found to benefit beetle species richness and composition, particularly that of carabids, and to a lesser extent staphylinids (Holmes *et al*., 1993; Dennis *et al*., 1998; Dennis *et al*., 2004; Mysterud *et al*., 2010). Vegetation structure will also respond to changes in grazing pressure at a faster rate than plant species composition (Marriott *et al*., 2004). However, others have found that vegetation height is not of great importance to beetles, as the majority reside at ground level, with only phytophagous species found crawling up the vegetation itself (Morris and Rispin, 1987; Tscharntke and Greiler, 1995).

Pterostichus diligens and *P. rhaeticus* are more common at higher altitudes, as has been found by other authors (Luff *et al*., 1989; Anderson, 1996; Abernethy *et al*., 1996; Luff, 1998). Rushton *et al*. (1991) observed that smaller species were less similar in their habitat preferences than larger species, with *P. vernalis* favouring the lowest altitudinal sites, *P. diligens* the highest and *P. strenuus* the intermediate. *Carabus clatratus*, although also more abundant in the uplands of the present study, was found almost exclusively on blanket bog (across a range of grazing states and altitudes), demonstrating the importance of this habitat type for rare or threatened species. In fact water-logged habitats, such as blanket bog, tend to be nutrient-poor, which helps to keep diversity high (Huston, 1979). Other *Carabus* spp. were also more abundant on blanket bog, as well as wet heath and dry siliceous heath. Williams and Gormally (2010) recommend *Carabus clatratus* as the strongest carabid indicator of blanket bog sites. In fact, although little is known of the ecology of many peatland carabid species, it is perhaps the draining of peatland rather than inadequate grazing management which poses the greatest threat to this rare species (Holmes *et al*., 1993; McFerran *et al*., 1995). *P. rhaeticus* is also known to be a species indicative of blanket bogs, primarily cut-over bogs (Williams and Gormally, 2010), while *P. diligens* is a peatland species, typical of very wet habitats (Butterfield and Coulson, 1983).

The specialist predator, *Notiophilus germinyi* was associated with traditional ewe grazing. This suggested a preference for a less intense/commercial level of grazing, a finding supported by the univariate analysis, which showed that a low sheep stocking rate of 0.21 - 0.40 LU/ha resulted in the greatest abundance of specialist carabid predators. Others have also found that *Notiophilus germinyi* preferred a less intensive management regime, reporting its detection in heather and rough grass, particularly in the uplands (Blake, 1996; Eyre and Luff, 2004), and, as a flightless habitat specialist, it may also be a good indicator of site quality and accessibility for other carabid species (Noordijk *et al*., 2008). *Notiophilus palustris*, however was more abundant on farms with a higher percentage of commercial ewes, perhaps suggesting a more intensive grazing regime, which was supported by the univariate analysis which showed that shorter vegetation was important for carabid specialists, and indeed others have observed that *Notiophilus palustris* has a preference for close grazed upland grassland (Butterfield and Coulson, 1983). In the present study, *Trechus obtusus* was more abundant at higher altitudes, with shorter vegetation, also supported by the univariate analysis. However this species is actually known to be widespread and abundant in many grassland and heath habitats across a range of altitudes (Anderson, 1996; Eyre and Luff, 2004; McCormack *et al*., 2009). *Cychrus caraboides* was most abundant in tall vegetation, at lower altitudes. Indeed this snail-eating species is known to be common in closed woodland canopy sites (Coll and Bolger, 2007), from the lowlands to the uplands (Harde, 1984), as well as in heathland. Others suggest that it is a species more abundant at higher altitudes (Anderson, 1996; Luff, 1998), where slugs replace the lowland diet of snails (McCormack *et al*., 2009). The specialist predators collected during this study consumed mainly Collembola, which are one of the most abundant soil organisms in most ecosystems (Bardgett and Cook, 1998). Soil pH is important for Collembolan survival (Coja *et al*., 2006), although it did not have a significant effect on specialist predators in the present study. They were, however, influenced to a large extent by altitude and % upland blanket bog, suggesting an indirect effect of soil pH. Carabid beetles which specialise on Collembola hunt using visual cues and therefore prefer a more open sward (Cole *et al*., 2006), as was evident for *Trechus obtusus*. Collembolan specialists, in the present study, were more common on wind-clipped montane heath than any other habitat, supporting the requirement for short vegetation for hunting. Upland blanket bog was also important, as was improved grassland in the lowlands, although abundance was greatest in the uplands. Ribera *et al*. (2001) and Cole *et al*. (2002) found that specialist predators, feeding on Collembola, were associated with intensively grazed lowland grassland, with shorter vegetation, due to the fact that Collembola are favoured by the application of inorganic and organic fertilisers and animals feeding on such a narrow range of prey species tend to synchronise their activity with that of their prey, while generalists do not (DeAngelis *et al*., 1975; Murdoch *et al*., 1985; Lövei, 2008). As in the present study, the authors also found that carabid specialists were more abundant in heather, suggesting that this was due to there being few other carabid species or individuals present in heathland (Cole *et al*., 2002). It may be that the higher abundance of specialists in the uplands of the present study was a reflection on heather cover and short vegetation as opposed to a preference for high altitudes. Indeed the dominance of *Calluna vulgaris* on a site, and its developmental stage has been found to be important for ground beetles (Gardner, 1991).

The phytophagous carabid, *Amara lunicollis*, was associated with low sheep stocking rates, tall vegetation and high scrub cover in the lowlands, indicating a preference for light levels of grazing. In fact phytophagous insect abundance and species richness has been shown to increase under low levels of grazing (Morris, 1981; Morris and Plant, 1983; Tscharntke and Greiler, 1995). *Amara plebeja* was found in areas of high soil pH (lowlands) and low % shrubs, suggesting it may have a preference for heavier grazing intensity (Dennis *et al*., 1997; 2004). Phytophagous beetles consume legumes and forbs, which are more prevalent in grazed areas, supressing aggressive competitive species (Gibson e*t al*., 1992; Woodcock et al., 2005). Both *Amara lunicollis* and *Amara plebeja* were also positively influenced by plant species diversity and % forbs. Phytophagous carabids were the only feeding group, in the present study, to be effected by plant species diversity, whilst generalist and specialist predators were influenced to a greater extent by plant functional diversity. Perhaps this is because phytophagous carabids rely directly on the plant species themselves, often being found on or near their food plants (Lövei and Sunderland, 1996), while predator carabids only rely indirectly on a particular species of plant (e.g. specialist predators of Collembola found near the roots of a Collembolan food plant). In fact phytophage species richness is known to be positively correlated with plant species richness (Tscharntke and Greiler, 1995; Harvey *et al*., 2008), which may decline with increased grazing or reseeding (Luff and

Rushton, 1989), suggesting that very light grazing would provide the ideal management regime for phytophagous carabids.

Studies have shown that the abundance and species richness of specialists declined with increasing disturbance (Magura *et al*., 2004), while generalist species were common in disturbed open grassland (Thies *et al*., 2003; van der Putten *et al*., 2004; Voigt *et al*., 2007; Lövei, 2008), where they were less sensitive than specialists to disturbances such as those caused by climate change (Thies *et al*., 2003; Hedlund *et al*., 2004). Habitat generalists, pioneer and invasive species are known to be more active in intensively grazed sites (Cole *et al*., 2005) and the worry is that overgrazing in the fragile grasslands of the uplands may lead to these species becoming dominant in these areas (Bohac and Slachta, 2008). Purtauf *et al*. (2005) found that carnivore species were highly sensitive to landscape change (requiring both a high amount of canopy cover and openness at ground level (Harvey *et al*., 2008)). Phytophages were less sensitive, although some suggest that it is the herbivorous species which may actually serve as sensitive indicators of changing climate, particularly through temperature (Hodkinson, 2005), while omnivores, which are insensitive to landscape change, (opportunistic generalists), have the ability to buffer environmental change by switching to alternative prey (Jørgensen and Toft, 1997; Holt *et al*., 1999). In fact, the abundant and species rich generalist predators may actually be redundant in their response to environmental change in that a decrease in the abundance of one species may be balanced by an increase in the abundance of another (Spencer, 2000; Raffaelli, 2004; Petchey *et al*., 2007; Vanbergen *et al*., 2010). Functional redundancy may, along with other regulating forces, promote ecological stability (Gerisch, 2012). An increase in habitat stability is thought to result in the loss of flight in carabids. Nilsson *et al*. (1993) found that carabids restricted to alpine or sub-alpine regions (altitudinal specialists) possessed large wings, while altitudinal generalists tended to have short or reduced wings, suggesting that higher altitudes provided less stable conditions. Contrary to findings in the present study, others have shown that phytophages and Collembolan specialists were associated with intensive management in the lowlands, whilst generalist predators were more numerous in the less intensively managed uplands (Ribera *et al*., 2001). Perhaps, as predators tend to be larger bodied, they require more substantial home ranges to meet their energetic demands and are therefore more sensitive to environmental change than species of lower trophic levels such as phytophages (Holt *et al*., 1999; Raffaelli, 2004). Other studies have found evidence to suggest that phytophagous species were more sensitive than predators to environmental change (Henle *et al*., 2004; Vanbergen *et al*., 2010) and management (Dennis *et al*., 2002; Allombert *et al*., 2005; Mysterud *et al*., 2010). Phytophages are known to be dependent upon the seeds of ruderal plants (Thiele, 1977) from disturbed areas (Ribera *et al*., 2001), suggesting that they are habitat specialists of open agricultural grassland (Vanbergen *et al*., 2010). Although, herbivorous carabids have been found to favour vegetation associated with dung patches, suggesting that their distribution may be patchy (Dennis *et al*., 1997), therefore making accurate sampling difficult (Cole *et al*., 2006).

Three of the five notable or locally distributed species found in this study were collected from above 460m. It has been suggested that populations of high altitude specialists are very small and isolated, making them vulnerable to environmental change (McCormack *et al*., 2006). A shift in the range of these carabid communities may lead to local extinctions (Butterfield, 1996; McCormack *et al*., 2006). Indeed studies have found that carabids have suffered serious biodiversity losses (Brooks *et al*., 2012), exacerbated by their wide-ranging roles within food webs (Lövei and Sunderland, 1996).

3.5.2 Grazing management and altitude

The interaction between grazing state and altitude at the habitat level indicates that carabids, staphylinids and other beetles respond to their environment at the fine scale. At the coarser farm level, carabid abundance increased as grazing intensity increased but declined as altitude increased and there was no interaction. Carabid beetles have been shown to respond more sensitively to disturbance at a fine scale than at the landscape scale (Niemelä *et al*., 1996; Dennis *et al*., 1998; 2002; Brose, 2003a; b; Vanbergen *et al*., 2005). Spatial scale has been shown to be most pronounced for carabid beetles at 1-3m and vegetation structure and composition appear more influential in predicting invertebrate assemblage structure than grazing at this scale (Cole *et al*., 2010). Tussocks in grassland were found to be associated with greater arthropod abundance and species richness than the inter-tussock sward (Dennis *et al*., 1998). The larger and more mobile the beetle, the larger the scale at which it perceives its landscape (Aviron *et al*., 2005; Holland *et al*., 2005) and this preference is generally based on food (Niemelä *et al*., 1992; 1996). Carabid abundance was considerably greater in the lowlands of habitats subject to a light, moderate or heavy grazing intensity, while habitats under the light-moderate and moderate-heavy grazing states exhibited greater carabid abundance in the uplands. This was also found to be true for generalist predators. Intermediate levels of grazing differed to other grazing states, in particular the moderate-heavy category, provided ideal conditions for carabids in terms of either vegetation structure or plant composition and diversity, alternatively habitats under this particular level of grazing might have attracted fewer specialist carabid species. Habitats under a heavier level of grazing, however, were more favourable for carabids at lower altitudes. A similar pattern is exhibited by staphylinid and other beetles, although only habitats subject to moderately-heavily grazing displayed an increase in other beetle abundance. As the patterns influenced the abundance of all beetles, we conclude that these patterns are real. However, although staphylinid abundance appeared to be affected by the same factors as carabid abundance, staphylinid species composition may differ substantially from that of carabids, as they are predominantly dependent upon dead wood, litter and moss, which accumulate under low levels of grazing (Good and Giller, 1991; Vanbergen *et al*., 2005). It is known that many staphylinid species are associated with dung (Coulson, 1988; Dennis *et al*., 2004) and so may be more common on highly grazed sites, although this was not found in the present study. Abundance was more sensitive than diversity indices to management and environmental factors, as found in other studies (Cole *et al*., 2006). It has been suggested that carabid assemblages are actually more sensitive than traditional diversity measures in detecting impacts of agricultural management (Cole *et al*., 2012b). In fact, variation in carabid assemblages may explain their differing responses to grazing state at different altitudes. Although the habitats subject to light-moderate and moderate-heavy levels of grazing did not appear to contain a greater number of upland species such as *Pterostichus diligens* or *P. rhaeticus*. In fact habitats under moderate-heavy levels of grazing were found at lower elevation to those of the other four states. The most likely explanation is that upland habitats which are grazed at intermediate (light-moderate and moderate-heavy) levels provide more suitable conditions for carabids than lowland habitats grazed at the same intermediate level, while lowland habitats subject to light, moderate and heavy categories of grazing are more suitable for carabids than upland habitats in the same grazing categories. Some studies have shown that grazing has no effect on arthropods and other invertebrates (Mysterud *et al*., 2005), but it does influence carabid beetles (García *et al*., 2009). Although grazing may have no effect on beetle diversity, it may influence beetle assemblage composition (Holmes *et al*., 1993; Woodcock *et al*., 2005; Cole *et al*., 2006). Some studies have shown that carabid and other arthropod abundance and diversity declined as grazing intensity increased (Morris, 1967; Luff and Rushton, 1989; Blake *et al*., 1996; Dennis *et al*., 1998; Mysterud *et al*., 2010). However, others have found that carabid species richness increased as grazing intensity increased (McFerran *et al*., 1994; Vanbergen *et al*., 2005; García *et al*., 2009), although there were differing effects on abundance, with some finding that carabid abundance increased with an increase in grazing intensity (García *et al*., 2009) and others finding no effect (McFerran *et al*., 1994). Factors such as sward type, the past history of a site (Blake *et al*., 1996; Dennis *et al*., 2004), altitude, plant species richness and functional plant richness have been found to influence carabid species to a greater extent than grazing management (Mysterud *et al*., 2005; Woodcock *et al*., 2005). In fact Cole *et al*. (2010) found that the amount of surrounding bracken and *Juncus* was influential in describing carabid assemblages, perhaps due to changes in humidity.

These results suggest that there is a very fine line between the best grazing management for the uplands and the lowlands in terms of maintaining and attracting carabid diversity. The two heaviest levels of grazing appear to encourage the greatest carabid abundance, however, too light or too heavy a level of grazing in the lowlands may result in a sharp decline in carabid abundance, whilst too light or too heavy a level of grazing in the uplands may also result in a large decline in carabid abundance. It appears that carabids in the uplands favour intermediate levels of grazing, while carabids in the lowlands favour the three main grazing categories. Therefore, below 200m, the ideal grazing intensity for carabid abundance would be high and above 200m the ideal grazing intensity would be in the moderately-heavy category.

Under the three main categories of grazing, it appears that only when altitudes of 600m are reached, do the benefits of a lighter grazing intensity become apparent. A moderate level of grazing appears to provide the most suitable conditions for carabid abundance at altitudes of between 200m and 600m. Although mechanisms for determining altitudinal variation in species richness are poorly understood (Hodkinson, 2005), this study has found that carabid abundance changes with altitude although it is clearly dependent upon grazing state, however, in general, there are fewer species at higher altitudes (Usher and Gardner, 1988; Butterfield, 1996). This does, however, differ with functional group. Predatory invertebrates show a decline with altitude while phytophagous species either increase or exhibit no trend with altitude (Coulson, 1988). Maveety *et al*. (2011) found that carabid species richness declined by one species with every 100m rise in elevation in the Peruvian Andes and the majority of species were restricted to only one altitudinal site. Butterfield (1996) also found little overlap between carabid species compositions at 450m and those at 800m on a mountain in northern England and suggested that this reflected the differing temperature regimes, although an increase in rainfall with altitude may explain some of the variation. Although a number of carabid species are more frequently found in the upland areas of Ireland and Britain, such as *Carabus glabratus* (Butterfield and Coulson, 1983), or the rare *Cymindis vaporariorum* (Goodier, 1968), both found in the present study, there are very few which are restricted to high altitudes. Holmes *et al*. (1993) did find a distinctive carabid assemblage in the uplands, however, this may have been as a result of unique upland habitats. Eyre *et al*. (2005) found that altitude was a poor predictor of ground beetle distribution, although this was dependent upon the scale at which the data was collected and an average altitudinal range of 50m has been found to be too small to detect altitudinal assemblage changes in beetles (Dennis *et al*., 1997).

3.5.3 Ecosystem services

It is important to acquire an improved understanding of SOC sequestration processes (Follett, 2001). By optimising agricultural management for the accumulation of SOC, atmospheric CO_2 may be sequestered, partially mitigating the current increase in atmospheric CO_2 (West and Post, 2002). Changes in agricultural practices aimed at increasing SOC should focus on increasing organic matter inputs into the soil, decreasing the decomposition of organic matter and increasing the amount of time during which the land is covered by growing plants (Paustian *et al*., 2000; Follett, 2001). Overall, in the present study, there was a positive trend in SOC as carabid abundance and species richness and other beetle abundance increased with soil moisture content at the farm level. Others have also found a positive correlation between the organic carbon content of the soil and carabid species richness, which was explained by the large variety of soil organisms in soil with high organic carbon content that provided a valuable food resource for carabids (Sądej *et al*., 2012). Heise *et al*. (2005) found that high concentrations of organic carbon in the soil may bind to plant protection compounds, thereby allowing plant-eating beetle species to safely consume the plants. Others have found no correlation between carabid distribution and soil parameters (Skalski *et al*., 2011). However, there is a very different picture at the habitat level, where SOC declines with an increase in carabid abundance and species richness across all grazing states, while SOC increases with carabid evenness across all states. SOC also increased with carabid abundance and soil moisture across all sheep stocking rates and declined with species richness on its own. This suggests that soil moisture may be driving these effects. Beetle abundance and species richness are known to be highly influenced by soil moisture (Gardner, 1991; Rushton *et al*., 1991; Bhriain *et al*., 2002) and the sites with greater moisture content perhaps contain more organic carbon, such as that of lowland blanket bog peats. However, carabid evenness was found to have the opposite effect on SOC to that of species richness or abundance. This has been noted by other authors, who found that evenness and richness in plant microcosms can be influenced by different processes and suggested that both diversity components should be measured whenever possible, and should be treated separately (Magurran, 1988). They found that richness was affected to a greater extent by the number of emerging seedlings (related to initial seed densities), while evenness was influenced more by species interactions such as competition (Wilsey and Stirling, 2007). Other studies, however, have found that the correlation between species richness and evenness was positive for animals and negative for plants (Stirling and Wilsey, 2001). Some have suggested that evenness may provide an insight into community function through disturbance such as grazing (McNaughton, 1977), and indeed the relationship between species richness and evenness has been shown to be positive under no grazing and negative on grazed sites (Manier and Hobbs, 2006). Beetle, spider and vegetation evenness has been shown to increase as management intensity declines (Perner and Malt, 2003) and organic farming has been suggested as a means of returning functional evenness to ecosystems (Crowder *et al*., 2010).

Carabids are known to be voracious feeders and consume close to their own body mass in food daily (Thiele, 1977). On heavily grazed farms there was a positive influence of carabid consumption and % scrub on Soil Organic Carbon (SOC). On lightly grazed farms there was a negative effect of carabid consumption and % scrub on SOC. While on lightly-moderately grazed farms SOC increased with carabid consumption, but decreased with % scrub. This suggests that grazing state does play an influential role in SOC levels and may prove to be important in carbon sequestration. Although, when the consumption rate and scrub interaction is taken into account, SOC decreases under all three levels of grazing, suggesting that perhaps % scrub is more important than grazing state in determining the effects of carabid consumption rate on SOC. Grazing may be important in preventing the succession of a site to a low productivity system, with low soil fertility. In this situation palatable plants would be replaced with unpalatable ones, which produce poor quality litter and have low rates of decomposition and nutrient release (Grime *et al*., 1996; Wardle *et al*., 2002; Bardgett and Wardle, 2003; Semmartin *et al*., 2010). Such an unproductive system may result in high rates of soil carbon sequestration (Bardgett and Wardle, 2003; De Deyn *et al*., 2008), further complicating the story. In this way, plant functional traits could be said to regulate soil carbon storage (De Deyn *et al*., 2008), driving ecosystem functions. However, while the indirect effects of herbivory on soil fauna via plant responses are important, the directions of these mechanisms are often unpredictable due to the involvement of several mechanisms acting on complex soil food webs (Bardgett *et al*., 1998b). In fact, studies have shown that SOC increased, decreased or remained unchanged under various grazing regimes, temperature and precipitation gradients (Piñeiro *et al*., 2010). Garnett *et al*. (2000) found no significant difference in the accumulation of carbon beneath grazed or ungrazed plots. Temperate grasslands have high SOC concentrations (De Deyn *et al*., 2008) and others have found that the organic carbon content of grassland soil increased with an increase in grazing pressure (Frank *et al*., 1995; Reeder and Schuman, 2002; Gao *et al*., 2007; Li *et al*., 2011). While Sun *et al*. (2011) actually found that increased grazing pressure reduced organic carbon content, being positively correlated with aboveground biomass and root biomass. They warn that heavy grazing can lead to a gradual change in grasslands from acting as ‘carbon sinks’ to becoming ‘carbon sources’, although this is thought to be season and site dependent (Milchunas and Lauenroth, 1993). Overgrazing may lead to the loss of litter and vegetation cover, and erosion may then be exacerbated by wind or trampling, leading to the loss of much SOC, which tends to be concentrated near the surface of the soil (Su *et al*., 2003; Worrall and Evans, 2009). Others also found that grazing depresses soil carbon content and storage (Snyman and Du Preez, 2005; Worrall *et al*., 2007; Wu *et al*., 2010).

The rise in SOC with the rise in % scrub on heavily grazed farms may indicate a lack of wet conditions in the bogs of heavily grazed farms, suggesting that they may have been drained for grazing land. Drainage has been shown to cause an increase in carbon production (Worrall and Evans, 2009). This drier peatland may now be less heavily grazed and consequently scrub encroachment is occurring. Coulson *et al*. (1995) notes that drainage of a site for less than five years alters the carabid fauna but has little effect on the staphylinids. Nonetheless, it may also reflect the fact that scrub tends to be woody in nature, containing species such as *Ulex* spp. and woody plants are known to reduce SOC (Post and Kwon, 2000).

Carabid consumption rate had a positive effect on SOC, but only under lightly-moderately and heavily grazed conditions. This suggests that undergrazing may actually have a negative effect on SOC, perhaps through reduced organic carbon inputs from manure (Post and Kwon, 2000; Milne, 2012) or maybe the lightly grazed sites contained a high proportion of woody plant species which are known to decrease SOC and are less effective than grasses at storing carbon in soil (Post and Kwon, 2000). This is contrary to general beliefs that overgrazing reduces SOC by increasing decomposition and therefore turnover time of carbon in soils (Chan, 2008). Previous management history can also have a large effect on carbon sequestration in soil (Post and Kwon, 2000), and this was not recorded in the present study. On lightly-moderately and heavily grazed farms the carabids may have had better access to Collembola prey and other soil invertebrates, and an increase in dung (on improved pasture) has been shown to increase Collembolan abundance, although there is a corresponding decrease in species richness (Stork and Eggleton, 1992; Dombos, 2001), while on lightly grazed farms perhaps the long vegetation inhibited access to these soil invertebrates. Collembolan presence is known to be associated with an increase in soil microbial biomass, which is stimulated by nutrients from dung and urine (McNaughton *et al*., 1997a; b; Bardgett *et al*., 1998a; Dennis, 2003). Trampling by too many livestock, particularly cattle, can lead to disturbance and compaction of the soil, reducing available daytime refugia in soil crevices for *Carabus* spp. (Dennis, 2003), which may increase soil pH through poor aeration, reducing Collembolan abundance (King and Hutchinson, 1976). Others have found that Collembolan abundance is positively correlated with the organic carbon content of the soil (Kovac and Miklisova, 1997; Devi *et al*., 2011). This process is, however, highly dependent upon soil moisture, temperature, pH and species-specific preferences of Collembola (Filser, 2002; Eaton *et al*., 2004; Devi *et al*., 2011), as well as host-specific Collembolan associations with particular plant species (and the fungi associated with their roots), found on impoverished soils such as those of bogs (Blackith, 1974). Collembola may also aid decomposition by consuming microflora and preventing its build up in the soil (Blackith, 1974). In fact, soil microorganisms play a central role in decomposition and respiration, thereby influencing the storage of carbon in the soil (Liu *et al*., 2012). The decomposer community on heavily grazed sites tends to be dominated by bacteria, while on lightly grazed or ungrazed sites fungi have a more prominent role in decomposition (Bardgett *et al*., 2001). This would suggest that fungi-consuming Collembola may be abundant on ungrazed sites. Staphylinids are also known to have a preference for litter, which attracts fungi under low or no grazing (Dennis, 2003). Grazing can modify the structure and function of ecosystems, which, in turn, can affect the storage of organic carbon in the soil (Piñeiro *et al*., 2010). Studies suggest that moderate grazing provides best balance between biodiversity, livestock production and soil carbon management (Li *et al*., 2011; Sun *et al*., 2011; Liu *et al*., 2012). Soil microbial biomass, has also been shown to be highest at intermediate levels of grazing intensity (Bardgett *et al*., 2001), although intensively managed systems tend to promote low soil faunal diversity (Bardgett and Cook, 1998).

The impact of insects on carbon dynamics is not well documented (Volney and Fleming, 2000). However, some studies have shown that climate change has resulted in the expansion in range of the mountain pine beetle in North America, which has led to a change in the forest from a carbon sink to a carbon source (Kurz *et al*., 2008). It would be expected that an increase in carabid consumption would lead to a rise in SOC and an enhancement of soil fertility through faecal pellets and burrowing (Brown *et al*., 2004), fuelling microbial growth and increased nutrient cycling (Hall, 2009). This was indeed the case when carabid consumption was correlated with SOC on its own. Heavy and moderate grazing resulted in an increase in SOC with consumption, however SOC decreased in lightly grazed sites, leading to the conclusion that grazing state does have an effect on SOC through carabid consumption. Nevertheless, an interaction between % scrub and consumption led to a general decline in SOC across all grazing states, suggesting that % scrub may be controlling this interaction. % scrub may also be an indicator of low soil moisture and as SOC tends to increase with soil moisture, this may be another explanation for the decrease in SOC with an increase in % scrub. Staphylinids, for example, favour wetter soil with a high organic matter content (Dennis, 2003). However the majority of carabids in the present study are generalist predators, so depending on the condition of an ecosystem, they may supplement their diet with a large number of fungi or bacteria, slowing decomposition, which may explain the lower levels of SOC through carbon sequestration (Hall, 2009), In fact Nietupski *et al*. (2010) found a negative correlation between predatory carabid species richness and organic carbon.

It has also been shown that the rate of carbon turnover decreases linearly with plant biomass (Brown *et al*., 2004), supporting the finding in the present study that SOC declined in lightly grazed sites, which contained higher plant biomass. Another explanation may be that lightly grazed sites tend to have greater numbers of wide-ranging large carabids whose influence was not picked up at the scale measured. It may also be explained by species assemblage or functional group effects, perhaps based on life cycles or habitat/feeding preferences of larvae. It is known that predator consumption rates follow a power-law increase with individual predator species body mass (Emmerson and Raffaelli, 2004; Brose *et al*., 2008) and indeed consumption rates are determined by rates of individual metabolism, which are dependent on body size and temperature (Brown *et al*., 2004). Body size is dependent upon species identity and therefore the loss of a particular species from an ecosystem may significantly influence the structure, stability and functioning of an ecosystem (Emmerson and Raffaelli, 2004). If a system is stable, energy consumption by large organisms should be suppressed, however, if the system is unstable then energy consumption is not dependent upon body size (Makarieva *et al*., 2004).

3.5.4 Further work

Carabids are abundant in agricultural fields worldwide and may act as important predators of agricultural pests (Lövei and Sunderland, 1996). However, as yet, there is little evidence of a strong pest management benefit of carabids in grasslands, although they have long been used to assess the quality of a habitat (Luff, 1996). Studies have found that the carabid species *Pterostichus madidus* and *Nebria brevicollis*, both highly abundant in the present study, showed a significant preference for *Calliphora* blowfly larvae (Mair and Port, 2001). Blowfly strike is the most prevalent ectoparasite-mediated disease to affect sheep in the UK and northern Europe (Snoep *et al*., 2002; Bisdorff and Wall, 2008), leading to welfare problems and significant losses in production. Incidence is significantly associated with higher mean rainfall and temperature (Broughan and Wall, 2007) and although strike was less prevalent at higher altitudes in adult ewes, an altitudinal relationship was not observed in lambs (Bisdorff and Wall, 2008). Current climate change scenarios predict an elongated blowfly season with earlier spring emergence and a higher incidence of fly strike (Taylor, 2012). The use of a biological control agent, such as the ground beetle, would enable a decrease on the reliance on insecticides (Tellam and Bowles, 1997). Granivorous and omnivorous carabids have also been shown to regulate the abundance of weed species in the seedbank (Bohan *et al*., 2011). *Pterostichus melanarius*, in particular, was found to regulate monocot weed species. This may be valuable in some upland areas where the unpalatable grass, *Nardus stricta*, dominates. Although seed predation increases with temperature (Saska *et al*., 2010), so perhaps consumption would be low in the cooler uplands. *Abax parallelepipidus* was found to be successful in controlling slugs on a grass/clover sward (Asteraki, 1993) and other carabids have been found to consume slug eggs and juveniles (Oberholzer and Frank, 2003; Tulli *et al.*, 2009). However generalist beetles are known to attack other prey in preference to adult slugs, only consuming slugs when slug density is high or other prey are unavailable, making them of limited use as pest control agents (Mair and Port, 2001).

The damaging effects of the heather beetle (*Lochmaea suturalis*) cause transition from heathland to grassland (Berdowski and Zeilinga, 1987; Tscharntke and Greiler, 1995), although changes seem to depend on initial vegetation and microclimate (Scandrett and Gimingham, 1991). Carabid beetle larvae have been found to consume the eggs of the heather beetle (Peterson *et al.*, 2004), although like the ladybird (*Coccinella hieroglyphica*), which is a known predator of the heather beetle, or parasites, it is unlikely to be present in sufficient numbers as to regulate heather beetle populations (Scandrett and Gimingham, 1991; Rosenburgh and Marrs, 2010).

3.6 Conclusions

This study has shown that grazing management and environmental factors play a significant role in determining carabid abundance, species richness and community composition and this was influenced by the composition of feeding groups within the carabid assemblage. Grazing management and environmental factors, as well as carabid abundance, species richness and consumption rate all had an effect on SOC. When grazing state was classified at the habitat level, the interaction between grazing and altitude helped to explain differences in beetle abundance and species richness, whilst, at the farm level this interaction also relied upon factors such as soil moisture or % scrub.

The intensification or abandonment of traditional farming practices throughout Europe has led to the loss of important habitats such as heather moorland or semi-natural grassland (Bignal and McCracken, 1996; 2000). This loss of extensive farming may threaten some of the rare carabid species found in this study (McCracken and Bignal, 1998). Although, evidence has shown that abandonment of grazing, even after 23 years, produced no significant loss in beetle species, there was a significant loss in plant species richness (Fadda *et al.*, 2008).

Although carabids are known to be affected to a greater extent by soil parameters than vegetation structure (Luff and Rushton, 1989), ground beetles that hunt using vision are influenced by vegetation structure (Cole *et al*., 2005). Some Collembolan feeders hunt by actively pushing through the leaf litter and if this layer is poorly formed, as in intensively grazed sites, these carabid specialists will be less abundant (Cole, *et al*., 2005).

Grazing pressure is particularly difficult to quantify. Wet areas such as bog may be left ungrazed, while drier ridges may be cropped to ground level. The selective nature of sheep grazing, combined with trampling and fertilisation, results in the creation of a biodiversity-enhancing mosaic, which provides different types of resources to support many arthropod species (Tscharntke and Greiler, 1995; Dennis *et al*., 2002). This type of grazing also promotes plant traits which aid slow carbon and nutrient cycling (Bardgett and Wardle, 2003), thereby the right management regime may have the potential to enhance the rate of carbon sequestration in the soil.

Rotational grazing as opposed to continuous grazing is recommended as being beneficial for both insect and plant diversity (Gebeyehu and Samways, 2003), preferably in short but intensive bursts every other year (Woodcock *et al*., 2005). The resulting difference in vegetation structure will consist of patches (0.70-4.73 ha) of tussocks and short sward (6-7 cm), preferably in a 1:1 ratio (Dennis, 2003), to encourage a larger overall number of beetle species (Dennis *et al*., 1997).

A change in carabid assemblage composition may affect ecosystem functioning (Cole *et al*., 2002). The importance of carabids as prey for farmland bird species such as skylarks (Poulsen *et al*., 1998), and lapwing (Johansson and Blomqvist, 1996), for example, may help to explain observed declines in farmland bird populations (Wilson *et al*., 1999). Light or moderate grazing regimes should create a heterogeneous mosaic of extensively grazed swards interspersed with short intensively grazed swards to provide the wide variety of conditions suitable for many different upland bird species (Fuller and Gough, 1999; Cole *et al*., 2010). The accessibility and detectability of invertebrates to birds is also vital (Vickery *et al*., 2001; McCracken and Tallowin, 2004; Cole *et al*., 2012a). This heterogeneity in agricultural habitats will help to support many species which require different environmental resources over time and scale, for circadian variation at the local level and seasonal variation at the landscape level, as well as enhancing their associated ecosystem services. In fact, the lack of success of current agri-environment schemes may be explained by their failure to consider landscape level environmental resources required by species' across their whole range (Kleijn and Sutherland, 2003; Cole *et al*., 2012b). Management aimed at preserving more open vegetation, may, in the long term, be of most value to carabid biodiversity (Brooks *et al*., 2012) and as carabids perceive their environment at fine scales, management at this level may also help to conserve ecosystem functioning (Brooks *et al*., 2012).

The present study has revealed the importance of grazing management, in conjunction with site-specific environmental factors, for carabids, staphylinids and other beetles, however, it has also highlighted the fact that changes in carabid beetle abundance and species richness can influence ecosystem functions such as the provision of food for birds, as well as the organic carbon in the soil. Soil organic carbon levels might suggest a potential impact on the ecosystem service of carbon sequestration.

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Chapter 4

The influence of upland grazing management on breeding bird density, diversity and species richness

Roslyn M. Anderson, Mark C. Emmerson, Mark W. Wilson and John O'Halloran

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Meadow pipit (*Anthus pratensis*) in bracken (*Pteridium aquilinum*)
(Photo: Isabelle Kozlik).

4.1 Abstract

The last 25 years have seen a dramatic decline in farmland bird populations across Europe. Much of this may be attributed to the process of agricultural intensification; however, with recent changes in the Common Agricultural Policy, land abandonment is also rapidly becoming a serious issue. The Irish uplands support many distinct and vulnerable habitats, internationally important for several unique bird species such as golden plover (*Pluvialis apricaria*) and ring ouzel (*Turdus torquatus*). A key feature of these upland areas is their openness, generally created by sheep or cattle grazing. Scrub encroachment, through a decline or cessation in grazing, may negatively affect species in these areas. This study investigated the impacts of grazing state, altitude and habitat on upland bird density, alpha diversity (Simpson's reciprocal index and bird species richness), evenness, beta diversity (complement of the Sorensen's similarity coefficient) (using LMM and GLMM) and gamma diversity (using ANOVA). Birds were sampled over two breeding seasons. Ninety six 1km transects were surveyed and 51 bird species recorded. While grazing state itself had no overall effect on transect-scale measures of bird density or diversity (although differences were observed at the regional scale), individual management factors such as % bare ground and % plant litter, for example, did. Altitude and habitat influenced bird density and diversity to the greatest extent. This study shows the importance of assessing grazing impact in the study of biodiversity. The challenge is to manage upland landscapes, along with their site-specific environmental characteristics, in a way that enhances biodiversity, maintaining the structural heterogeneity of the vegetation, along with a mosaic of habitat types to encourage a variety of bird and other wildlife species. Appropriate management should promote ecological diversity across a range of scales, altitudes, habitats and grazing states, whilst also integrating the decisions of peoples living and working in these marginal areas.

4.2 Introduction

In many parts of Europe extensive pastoralism has coexisted with its surrounding environment for centuries (Kleijn *et al*., 2006) and, although no European mountain is now truly natural, the resulting semi-natural habitats do support a diversity of unique plant and animal species (MacDonald *et al*., 2000). In the mid twentieth century agricultural specialisation and intensification began to replace the more traditional mixed farming systems. As production became the priority, the Common Agricultural Policy (CAP) subsidies saw a substantial growth in sheep (*Ovis aries*) numbers in both the uplands and lowlands, along with a corresponding decrease in cattle (*Bos taurus*) numbers in the uplands (Robson, 1997; Fuller and Gough, 1999; Dennis, 2003). Farmland now constitutes around 45% of the total land area of Europe (Food and Agriculture Organization of the United Nations, 2011) and therefore plays a major role in shaping the European landscape. In some areas, such as the Mediterranean, it has been shown that for decades CAP measures have actually intensified production in the more fertile lowlands, whilst increasing abandonment in the uplands (Caraveli, 2000; Matthews *et al*., 2006). Agricultural areas are home to more than half of all European bird species and fifty percent of these are either threatened or internationally important. The rise in agricultural intensification in lowland systems has led to a dramatic decline in farmland bird populations (Donald *et al*., 2001; 2006; Nikolov, 2010), and yet few studies have focused on the effects of grazing intensity on upland bird populations (Anderson and Yalden, 1981; Thompson *et al*., 1988; Fuller and Gough, 1999; Critchley *et al*., 2004; Marriott *et al*., 2004; Pollock *et al*., 2005). The limited understanding of trends in upland ecosystems results from the lack of adequate monitoring as well as insufficient habitat-specific information on any changes in grazing pressure (Fuller and Gough, 1999). Therefore the consequences of changing land use management in upland systems remain largely unexplored. The effects of land abandonment and undergrazing on bird populations has received far less attention than the effects of overgrazing (Tucker, 1997; MacDonald *et al*., 2000; Suárez-Seoane *et al*., 2002; Laiolo *et al*., 2004; Báldi *et al*., 2005; Brambilla *et al*., 2007; Sirami *et al*., 2007; Sirami *et al*., 2008; Nikolov, 2010). Undergrazing or the “under-utilisation” of land becomes evident when scrub or coarse vegetation reaches environmentally detrimental levels, while overgrazing occurs when high numbers of livestock adversely affect the growth, quality or diversity of vegetation (Department for Environment, Food and Rural Affairs, 2011). This polarisation of agricultural practices, intensification in the lowlands and abandonment in the uplands, is likely to threaten the biodiversity of semi-natural habitats. For example, it has been estimated that 14% of the habitats listed in the Habitats Directive may actually be threatened by agricultural abandonment (Bignal and McCracken, 1996; Ostermann, 1998). To address this deficit of information, this study is focussed on quantifying biodiversity changes resulting from modifications in management practices and the consequences for upland bird species.

The introduction of the Single Payment Scheme (SPS) by the EU in 2005 saw the decoupling of direct payments from production and a reduction in the incentive to maintain high stocking rates (Gardner *et al*., 2009; O'Rourke, 2009). This substantial CAP reform saw a welcome reduction in overgrazing in many regions. However it also had negative consequences for the landscape of marginal areas, resulting in a decline in farming, a substantial rise in undergrazing, a loss in habitat heterogeneity and a reduction in biodiversity value (Farina, 1997; Benton *et al*., 2003). In these circumstances, had it not been for the buffering effects of national agri-environment schemes, many areas would very likely have become abandoned (Brady *et al*., 2009; Acs *et al*., 2010).

All member countries of the EU are required to develop and implement agri-environment schemes. However, there is strong debate over whether or not these schemes are effective in enhancing ecological diversity (Kleijn *et al*., 2001; Peach *et al*., 2001; Kleijn and Sutherland, 2003; Bradbury *et al*., 2004; Vickery *et al*., 2004; Rath *et al*., 2005; Tscharntke *et al*., 2005; Kleijn *et al*., 2006). For example, a range of recent studies (Purvis *et al*., 2005; Bracken and Bolger, 2006; Kleijn *et al*., 2006; Brady *et al*., 2009; Nikolov, 2010) have shown that agri-environment schemes benefit common species, but have little effect on uncommon or endangered species, suggesting a clear need for integrated evaluation and monitoring on a more locally targeted county or regional basis. The present study will highlight management decisions and environmental factors important for upland bird species, with the view to integrating this information into focused agri-environment schemes.

No statutory definition of the uplands exists. However the use of the term 'upland' by Ratcliffe (1977) and Ratcliffe and Thompson (1988), referring to those areas lying 'typically above the limits of enclosed farmland' and at altitudes above 200m (Thompson *et al*., 1995; Milne, 1996) are very similar to the definition of mountains by the European Commission Council Regulation 1257/99 (Article 18). There is general consensus over the unique nature of these environments, their physical and economic remoteness and extreme climatic conditions, although debate exists over the relative importance of particular species and habitats (Brown and Stillman, 1993) and the degree of endemism (Thompson *et al*., 2005). Altitudinal zonation in mainland Europe is generally defined by the climatic effects, such as temperature, on mountain vegetation (Poore and McVean, 1957; Horsfield and Thompson, 1996; Körner *et al*., 2011; Pecher *et al*., 2011). The uplands contain many distinct and vulnerable habitats such as blanket bog, heath and moorland, often dominated by ling

(*Calluna vulgaris*). These ecosystems are internationally important for many unique bird species including golden plover, ring ouzel, red grouse (*Lagopus lagopus scotica*) and raven (*Corvus corax*). They also support high densities of meadow pipit (*Anthus pratensis*) and skylark (*Alauda arvensis*) (Crowe *et al*., 2010; Crowe, 2011; Copland *et al*., 2012), and provide locally important breeding habitat for wren (*Troglodytes troglodytes*). In fact twenty percent of the bird assemblage associated with upland heather moorland in the UK is listed under Annex 1 of the EC Directive on the Conservation of Wild Birds, 79/409/EEC. Inclusion of a species on this list requires the designation of their associated habitat as a Special Protection Area (SPA). 40% of the forty bird species associated with moorland are in decline and five of those have been affected by grazing pressure (Thompson *et al*., 1995), although there is much debate over how these birds will be influenced by specific changes in habitat (Usher and Thompson, 1993; Brown and Bainbridge, 1995; Thompson *et al*., 1995).

The present study assessed the impacts of grazing state on upland bird species density, diversity, species richness and evenness between transects and regional diversity across farms. The aims of the study were (i) to investigate whether upland bird species showed preferences for high, moderate or low grazing management intensities, (ii) to identify the relative effects of altitude on upland bird species and (iii) to identify the relative effects of habitat diversity and type, as well as vegetation structure on upland bird species.

4.3 Methods

4.3.1 Study area

The Iveragh Peninsula (51° 94´ N, 9° 89´ W) in County Kerry, southwest Ireland, covers almost 1400km^2, and is surrounded on three sides by the Atlantic, making it the most geographically isolated peninsula in Ireland (Crowley and Sheehan, 2009). The dominant rock type is old red sandstone (Higgs, 2009) and the majority of soils are nutrient deficient peaty podzols and blanket peats, which, along with a high annual rainfall of over 1500mm, give rise to the vast blanket bogs and heaths which typify the area (**Table 4.1**) (Carruthers, 1998; Averis *et al*., 2004; Crowley and Sheehan, 2009). Approximately 65% of the peninsula may be classified as upland (O'Rourke and Kramm, 2009). Land use in these marginal areas is limited and is presently dominated by hill sheep farming.

Seven geographically distinct study areas within Iveragh were selected based on their potential for continuation in extensive hill farming. Within each of these areas, three hill farms were identified which represented a gradient of grazing management intensity. Farm hill land reached altitudes of between 400m and 800m, although total farm areas were generally less than 250ha. Sheep stocking rates ranged from 0.06 – 0.76 LU/ha over the whole farm and 0.005 – 0.48 LU/ha in the uplands.

Table 4.1 Distribution of habitats across farms.

Habitat	Habitat code	Occurrence (number of farms)	
		2007	2008
Improved grassland	1	10	12
Wet grassland	2	2	1
Dry humid acid grassland	3	6	7
Lowland blanket bog	4	7	7
Upland blanket bog	5	8	10
Eroding blanket bog	6	1	0
Wet heath	7	4	5
Montane heath	8	2	2
Dry siliceous heath	9	3	1
Scrub	10	2	3
Woodland edge	11	1	0
Bracken	12	2	0

4.3.2 Grazing state classification

Each farm consisted of a heterogeneous mosaic of fields and habitats subject to a range of grazing intensities. Following an initial farm visit, all habitats within each farm were mapped (Fossitt, 2000; Hill *et al*., 2005). Adopting the standard method of MacDonald *et al.* (1998), the impacts of grazing, browsing and trampling by large herbivores in upland habitats were quantified. A series of directly observable habitat-specific field indicators, including sward height and structure, accumulation of dead plant material (litter), cover of bare ground, selectivity of grazing and presence of dung, were used. For each field indicator light, moderate and heavy (L, M and H, respectively) impact categories were used to evaluate the alternative states. An overall estimation for a particular habitat type was then derived by assessing each field indicator separately using a number of point estimates or quadrats.

In order to account for spatial heterogeneity, a method of summarising the impact across a habitat was devised, using the percentage of the area occupied by each impact class (Agresti, 1984; Brewer *et al*., 2004; Albon *et al*., 2007). This resulted in the smoothing of the three class impact scale into a more continuous five point scale by introducing intermediate classes light/moderate (L/M) and moderate/heavy (M/H) (**Table 4.2**) (after Albon *et al*. 2007). Others have adopted a similar system by allocating weightings to each L, M or H indicator in order to arrive at a numerical sum for each surveyed area (O'Hanrahan, 2005).

Table 4.2 Distribution of farms across grazing states.

	Grazing state				
Year	Light	Light-moderate	Moderate	Moderate-heavy	Heavy
2007	4	4	0	0	4
2008	2	3	3	0	4

ArcGIS 9.3 (2008) was used to digitise habitat maps for each farm, which allowed the calculation of explanatory variables such as habitat diversity (Shannon-Wiener Index) and altitude. The habitat maps also enabled the association of habitat type and other environmental variables with each bird transect. Environmental data was collected, including plant species richness (133 plant species were recorded in total using Braun-Blanquet percentage cover estimates), vegetation height (cm), soil depth, soil pH and soil moisture. In total, 144 2m x 2m quadrats were sampled on twelve farms in 2007 and a further 108 quadrats from an additional nine farms in 2008. The fine scale plant quadrat data was also used to provide an independent assessment of grazing impact within each habitat type per farm.

4.3.3 Bird surveys

Bird counts were undertaken between April and June in 2007 and 2008. Each farm was surveyed twice, an approach based on the integration of the methodologies of the Breeding Bird Survey (Newson *et al*., 2009) and the Countryside Bird Survey (Coombes *et al*., 2006; Crowe *et al*., 2010) and Bibby *et al*. (1992). The survey route comprised two 1km transects, one below 200m in altitude and one above 200m, the transects were situated about 500m apart. Counts were not undertaken in conditions of rain or strong winds and commenced an hour after sunrise to avoid the dawn peak in bird activity (Herzon and O'Hara, 2007). For each transect the maximum count of individuals from the two visits (from first and second surveys) was chosen for analysis (Brown and Stillman, 1993; Browne *et al.*, 2000; Pearce-Higgins and Grant, 2006; Herzon and O'Hara, 2007). The sequence in which transects were walked was reversed between visits in order to minimise any bias in time of day surveyed.

All individuals seen and/or heard, and their perpendicular distance from the central transect line, were assigned to one of three distance categories: 0-25m, 25-100m and 100-300m and recorded on maps (Vanhinsbergh and Chamberlain, 2001). Actual distances were only recorded in 2008. Data gathered in 2007 were assigned an average distance, corresponding to the mid-point of each distance class, so that Group 1 was 12.5m, Group 2 was 63m and Group 3 was 200.5m. Distance sampling software (Buckland *et al.*, 1993; DISTANCE Version 5) was used to estimate bird densities. To account for any inter-annual variation, and to maximise the size of the study area, three farms from 2007 (one from each of the grazing states classified using MacDonald *et al.*, 1998 and Albon *et al.*, 2007) were again surveyed in 2008. The total density (birds/ha), Simpson's reciprocal index (alpha diversity; Magurran, 1988), species richness (alpha diversity), evenness, the complement of Sørensen's similarity coefficient and a measure of compositional change or species turnover (beta diversity; Magurran, 1988; Jost, 2007; Jurasinski and Kreyling, 2007; Benavides and Quesada, 2011) and regional (gamma) diversity were calculated (Lande, 1996; Jost, 2007).

4.3.4 Data analysis

Whittaker (1972) described alpha (α), beta (β) and gamma (γ) diversity as the diversity within plots, between plots and at the landscape level, respectively. The total species diversity in a set of communities can be partitioned into additive components within and between communities (Lande, 1996), allowing the calculation of alpha, beta and gamma diversity across a range of spatial scales (Gering *et al.*, 2003).

Species richness, as the total number of species in a sample, is the most widely used measure of alpha diversity due to its simplicity (Lande, 1996) and was used in the present study, along with Simpson's reciprocal index to quantify alpha diversity within each transect:

$$D = 1 / \Sigma P_i^2$$

Where P_i is the relative density of species $_i$. Simpson's reciprocal index, however, cannot be divided into additive components (Lande, 1996), therefore beta diversity, the amount of compositional change in a set of samples, such as species turnover along an environmental gradient (Lennon *et al*., 2001), was quantified using the complement of the Sørensen similarity coefficient (1 - βsim) (Jurasinski and Kreyling, 2007). Specifically, the index was used to calculate the dissimilarity in species composition between transects using bird density (Jankowski *et al*., 2009; Marsh *et al*., 2010):

$$\text{Sør} = 2j_N / (a_N + b_N)$$

Where a_N is the total species density from all transects, b_N is the total species density from the focal transect and j_N is the sum of the minimum density for each species between the focal transect and all other transects (Jankowski *et al*., 2009). This index has been shown to be one of the most suitable similarity indices available (Magurran, 1988; 2004).

Regional or gamma diversity was estimated as the pooled bird species richness across farms. Density was measured as the number of individual birds per hectare, while evenness was calculated by dividing Simpson's reciprocal index by the maximum value Simpson's could take (i.e. total species richness):

$$E_D = D / D_{max}$$

The underlying assumptions of normality, heterogeneity of variance, detection of outliers and collinearity of explanatory variables were assessed after Zuur *et al*. (2010). All analyses were conducted using ANOVA, linear mixed effects models (LMMs) or generalised linear mixed models (GLMMs) to accommodate deviations from normality or heterogeneity of variance (Bolker *et al*., 2009). All analyses were performed using R, version 2.12.1 (R Development Core Team, 2010), using the packages 'nlme' (Pinheiro *et al*., 2010) and 'lme4' (Bates & Maechler, 2010). The structure of the linear mixed effects models of bird density, Simpson's alpha diversity, evenness and beta diversity, the generalised linear mixed models of bird species richness and the ANOVA models of gamma diversity are shown in **Table 4.3**.

Variance inflation factors (VIFs) were used to select only those explanatory variables which were not collinear (Zuur *et al*., 2009; Zurr *et al*., 2010). In a stepwise procedure, the variable with the highest VIF at each step was removed until a final selection of explanatory variables was retained, all retained variables had a VIF of less than three (Zurr *et al*., 2010). A linear regression model was then employed to account for variation in measures of bird density and diversity using explanatory variables retained by the VIF procedure. The lowest Akaike's information criterion (AIC) and stepwise deletion procedures were used to select each model. Any variable retained was assumed to contribute to the pattern of the data. The transect-scale data did not meet the linear regression assumption of independence (clear patterns existed between the response variables and spatial variables such as area and farm), therefore a linear mixed effects model with residual maximum likelihood estimation (REML) was adopted. LMMs quantify the variation in the intercept caused by differences between factor levels of the random effects by estimating the distribution of the means instead of estimating a mean for every single factor level, thereby reducing the number of degrees of freedom used up by the factor levels (Crawley, 2007). The final model was fitted with generalised least squares (gls) to allow a comparison with the equivalent LMM.

Table 4.3 Model structures and associated variables (* indicates interaction between variables).

Year	Response variable	Fixed effects								Random effects		
2007	density	state +	altitude +	rock +	moisture *	forbs *	plant species richness			site	farm	
2008	$\log_{10}$ density	state +	$\log_{10}$ altitude +	habitat						site	farm	
2007	$\log_{10}$ α-diversity	state +	altitude +	habitat +	moisture +	graze +	litter +	forbs +	habitat richness	site	farm	
2008	$\log_{10}$ α-diversity	state +	$\log_{10}$ altitude +	habitat						site	farm	
2007	species richness	state +	altitude +	habitat +	litter +	shrubs				site	farm	transect id
2008	species richness	state +	altitude +	habitat						site	farm	transect id
2007	$\log_{10}$evenness	state +	altitude +	graze +	forbs +	plant species richness				site	farm	
2008	evenness	state +	sqrt rock +	sqrt dung +	habitat richness					site	farm	
2007	β-diversity	state +	habitat +	moisture +	litter +	plant species richness				site	farm	
2008	β-diversity	state *	$\log_{10}$ altitude +	sqrt graze *	sqrt bare ground					site	farm	
2007	γ-diversity	state +	litter									
2008	γ-diversity	state +	graze+	litter								

Density, Simpson's alpha diversity and associated estimates of evenness and beta diversity, all represent continuous integer data and therefore it is not appropriate to analyse these data using an alternative error structure such as Poisson. Consequently, we used a log transformation of the response variables, bird density and Simpson's alpha diversity from the 2008 data and Simpson's alpha diversity and evenness from the 2007 data. We also used a log transformation of the explanatory variable altitude and a square root transformation of % dung, % rock and % signs of grazing for some of the models. Raw values of density (2007), evenness (2008) and beta diversity in both years were analysed. Species richness, as count data, was not log-transformed (O'Hara and Kotze, 2010), instead, a Poisson error term was used to analyse patterns of bird species richness, using a GLMM (Bolker *et al*., 2009). Transect identity (10 levels) was added to this model as an observation-level random effect, in order to account for a small amount of overdispersion (Benjamin Bolker, pers. comm.). After meeting the assumptions of normality, homogeneity and independence (Zuur *et al*., 2010), gamma diversity was analysed using a two-way (2007) and three-way (2008) ANOVA.

Grazing state (5 possible categories), altitude (continuous in metres), habitat (12 levels), the continuous % of: signs of grazing, vegetation litter, dung, bare ground, rock, soil moisture, forbs, shrubs and plant species richness (count, ranging from 4 – 26 species) and habitat richness (count, ranging from 8 – 18 habitats, including water bodies and smaller habitats not individually sampled as part of the 12 surveyed habitats) were analysed as fixed effects. Farm (21 levels) was nested within area (7 levels), and therefore both were treated as random effects. Because of overlap in farms between 2007 and 2008 the two data sets were analysed separately. The baseline grazing state and habitat type were changed successively in order to test for differences between all states and habitats.

Model simplification was undertaken and the minimal adequate model chosen. Model validation was carried out and homogeneity checked through the use of plots of model residuals versus fitted values and model residuals versus all explanatory variables. Model normality was assessed using QQ-plots and histograms of the residuals, in conjunction with the Shapiro-Wilk test. REML was used to estimate the random effects terms and Maximum Likelihood (ML) was used to quantify the fixed effects. Each interaction was systematically compared with the whole model using the likelihood ratio test (Zuur *et al*., 2009). Terms which led to a significant reduction in explanatory power after removal were retained (through comparison of the AIC). In some instances model validation (for normality of residuals and homogeneity of variance) led to the retention of non-significant interaction terms in the final model. The AICc, ΔAIC, Akaike weights and evidence ratios were used in decisions regarding two similarly adequate models.

Parameter estimates and standard errors only are reported for the LMMs and GLMMs, as the associated p-values can be unreliable (Baayen *et al*., 2008). P-values, calculated using the anova function (sum of squares), are used instead to assess the significance of variables. This procedure also produces *F*-statistics and numerator and denominator degrees of freedom. The unbalanced nature of the data in the present study and the non-significance of the two-way interaction terms in the majority of models, demonstrated the importance of the main effect terms. As the order of variables in the model is important when using sequential sum of squares (Zuur *et al*., 2009; Hector *et al*., 2010), it was concluded that Type III Sum of Squares should be employed. The use of Type III Sum of Squares whilst controversial (Hector *et al*., 2010), was therefore considered justified on this occasion.

4.4 Results

4.4.1 Effect of grazing state on bird density and diversity

4.4.1.1 Density

There was no evidence to suggest an overall effect of grazing state on bird density in 2007 (**Fig. 4.1**) ($F_{2,6}$: 0.138, $p = 0.874$), however there was a negative effect of altitude (**Fig. 4.3**) ($F_{1,99}$: 44.96, $p < 0.0001$), with lower density in the uplands (estimate –0.022 ± s.e. 0.003). Areas containing a higher % bare ground also saw lower bird densities (estimate –0.185 ± s.e. 0.04).

In 2008 bird density was significantly higher in the moderately grazed state 3 than in the heavily grazed state 5 (estimate –0.24 ± s.e. 0.048), however, there was no evidence to suggest an overall effect of state on bird density ($F_{3,3}$: 8.76, $p = 0.054$) (**Fig. 4.2**). Bird densities were clearly affected by altitude (**Fig. 4.4**) ($F_{1,101}$: 31.33, $p < 0.0001$), with the lowlands exhibiting significantly higher bird densities than the uplands (estimate –0.723 ± s.e. 0.129).

Habitat type also played a substantial role in determining bird density, with improved grassland and scrub containing the greatest densities and upland blanket bog and heath, the lowest ($F_{6,101}$: 11.09, $p < 0.0001$; see **Appendix A S4.1** and **S4.2** for pairwise comparisons between habitat types in 2007 and 2008, respectively).

4.4.1.2 Simpson's alpha diversity

There was no evidence to suggest an overall effect of grazing state on Simpson's diversity in 2007 (**Fig. 4.1**) ($F_{2,5}$: 0.64, $p = 0.567$). An altitudinal effect ($F_{1,92}$: 31.62, $p < 0.0001$), however, was clearly demonstrated, with higher Simpson's diversity in the lowlands than in the uplands (estimate –0.001 ± s.e. 0.0002) (**Fig. 4.3**). Habitat type, again, was also important ($F_{11,92}$: 2.94, $p < 0.01$).

Grazing state showed no indication of an effect on Simpson's diversity in 2008 (**Fig. 4.2**) ($F_{3,3}$: 4.60, $p = 0.121$). However, both an altitudinal effect ($F_{1,101}$: 36.65, $p < 0.0001$), with significantly higher Simpson's diversity in the lowlands than in the uplands (estimate –0.677 ± s.e. 0.112) (**Fig. 4.4**) and a habitat effect were found ($F_{6,101}$: 9.51, $p < 0.0001$).

4.4.1.3 Species richness (alpha diversity)

Bird species richness was not affected by grazing state in 2007 (**Fig. 4.1**) ($F_{2,6}$: 3.65, $p = 0.092$). An altitudinal effect, however, was apparent (**Fig. 4.3**) ($F_{1,94}$: 18.73, $p < 0.0001$), with lower bird species richness in the uplands (estimate –0.002 ± s.e. 0.0005). Habitat type, again, was highly influential ($F_{11,94}$: 4.09, $p = 0.0001$). There was a significant difference in bird species richness between the habitats of lightly grazed farms ($F_{8,25}$: 2.68, $p = 0.03$) and heavily grazed farms ($F_{5,28}$: 2.85, $p = 0.034$) but not between the habitats of lightly-moderately grazed farms ($F_{5,28}$: 0.99, $p = 0.444$) (**Fig. 4.5**). The % vegetation litter had an effect on species richness ($F_{1,94}$: 5.88, $p = 0.017$), however, unexpectedly, it was those sites containing higher levels of litter which gave rise to greater bird species richness (estimate 0.002 ± s.e. 0.002).

Although there was no overall effect of grazing state on bird species richness in 2008 ($F_{3,3}$: 5.46, $p = 0.099$) (**Fig. 4.2**), the moderately grazed state 3 exhibited higher species richness than the lightly grazed state 1 (estimate 0.278 ± s.e. 0.122), lightly-moderately grazed state 2 (estimate 0.398 ± s.e. 0.112) and heavily grazed state 5 (estimate 0.356 ± s.e. 0.094). This suggests that bird species richness is affected to a greater extent by grazing state than either density or Simpson's diversity. Again, an overall altitudinal effect was clearly demonstrated (**Fig. 4.4**) ($F_{1,101}$: 23.28, $p < 0.0001$), with greater species richness in the lowlands than the uplands (estimate – 0.003 ± s.e. 0.0006). Habitat also had a significant effect ($F_{6,101}$: 6.91, $p <$ 0.0001). There was a significant difference in bird species richness between the habitats of lightly-moderately grazed farms ($F_{5,21}$: 3.44, $p = 0.02$) and heavily grazed farms ($F_{4,31}$: 13.33, p < 0.0001) but not between the habitats of lightly grazed farms ($F_{4,13}$: 1.77, $p = 0.194$) or moderately grazed farms ($F_{3,23}$: 1.22, $p = 0.327$) (**Fig. 4.5**).

4.4.1.4 Evenness

In 2007 there were no significant effects of state (**Fig. 4.1**) ($F_{2,6}$: 0.28, $p = 0.768$) or altitude (**Fig. 4.3**) ($F_{1,104}$: 1.14, $p = 0.289$) on bird evenness and also no significant effects of state in 2008 (**Fig. 4.2**) ($F_{3,2}$: 2.90, $p = 0.267$). % forbs, however, in 2007 was influential ($F_{1,104}$: 8.61, p < 0.01), with areas containing greater forb coverage showing greater bird evenness (estimate 0.002 ± s.e. 0.0005).

4.4.1.5 Beta diversity (1 - Sørensen's similarity coefficient)

There was no evidence to suggest an overall effect of grazing state on beta diversity in 2007 ($F_{2,6}$: 2.19, $p = 0.193$). There was, however, a clear effect of habitat on beta diversity ($F_{11,94}$: 2.41, $p = 0.011$), as well as a positive influence of % soil moisture ($F_{11,94}$: 2.41, $p = 0.011$), with wetter sites having greater similarity (and therefore lower beta diversity) (estimate 0.003 ± s.e. 0.0009). The % vegetation litter ($F_{11,94}$: 2.41, $p = 0.011$) had a negative effect on similarity and therefore a positive effect on beta diversity) (estimate –0.001 ± s.e. 0.0003), while plant species richness ($F_{11,94}$: 2.41, $p = 0.011$) had a positive influence on similarity (estimate 0.007 ± s.e. 0.002) (negative effect on beta diversity).

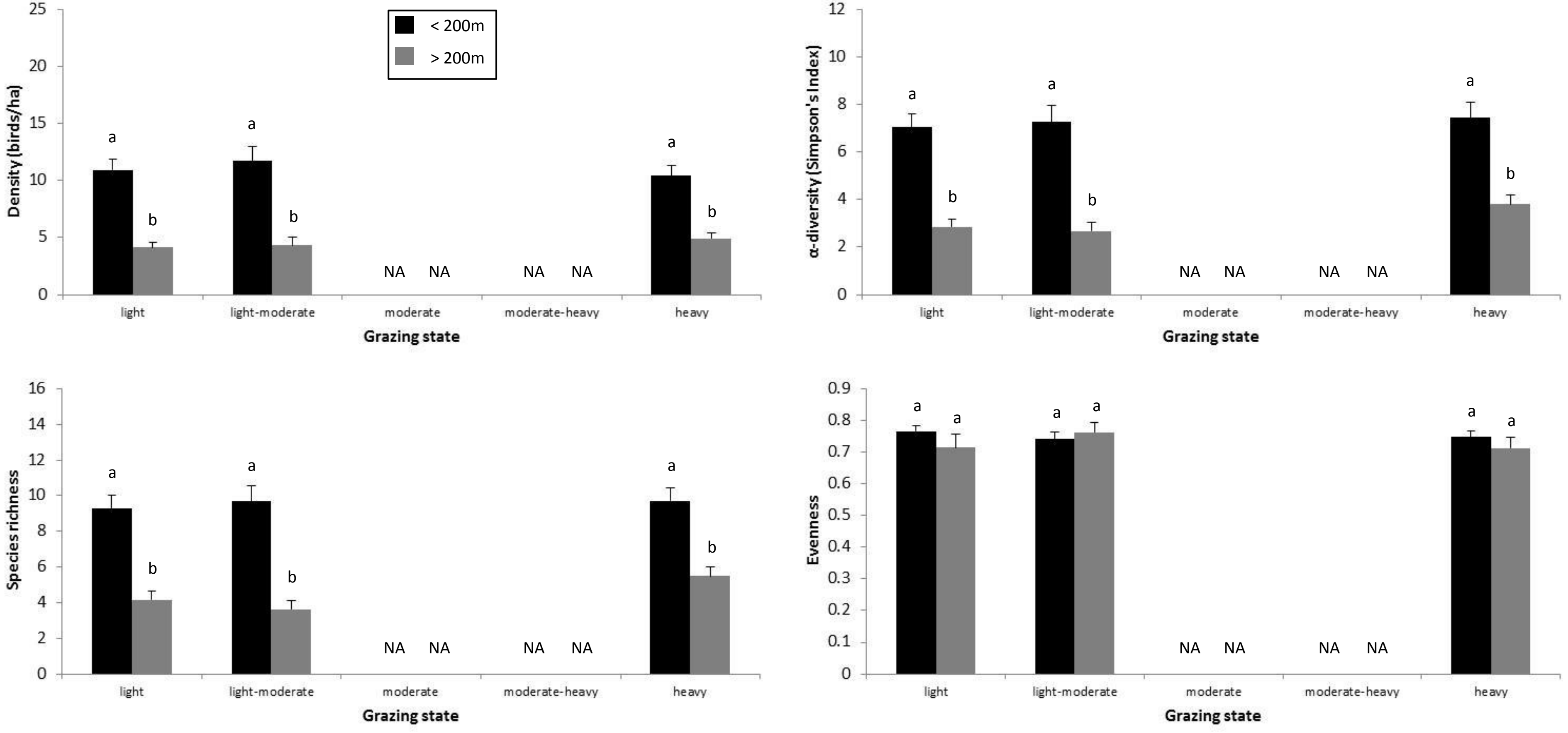


Fig. 4.1 Mean bird density, Simpson's alpha diversity, species richness and evenness across grazing state (2007).

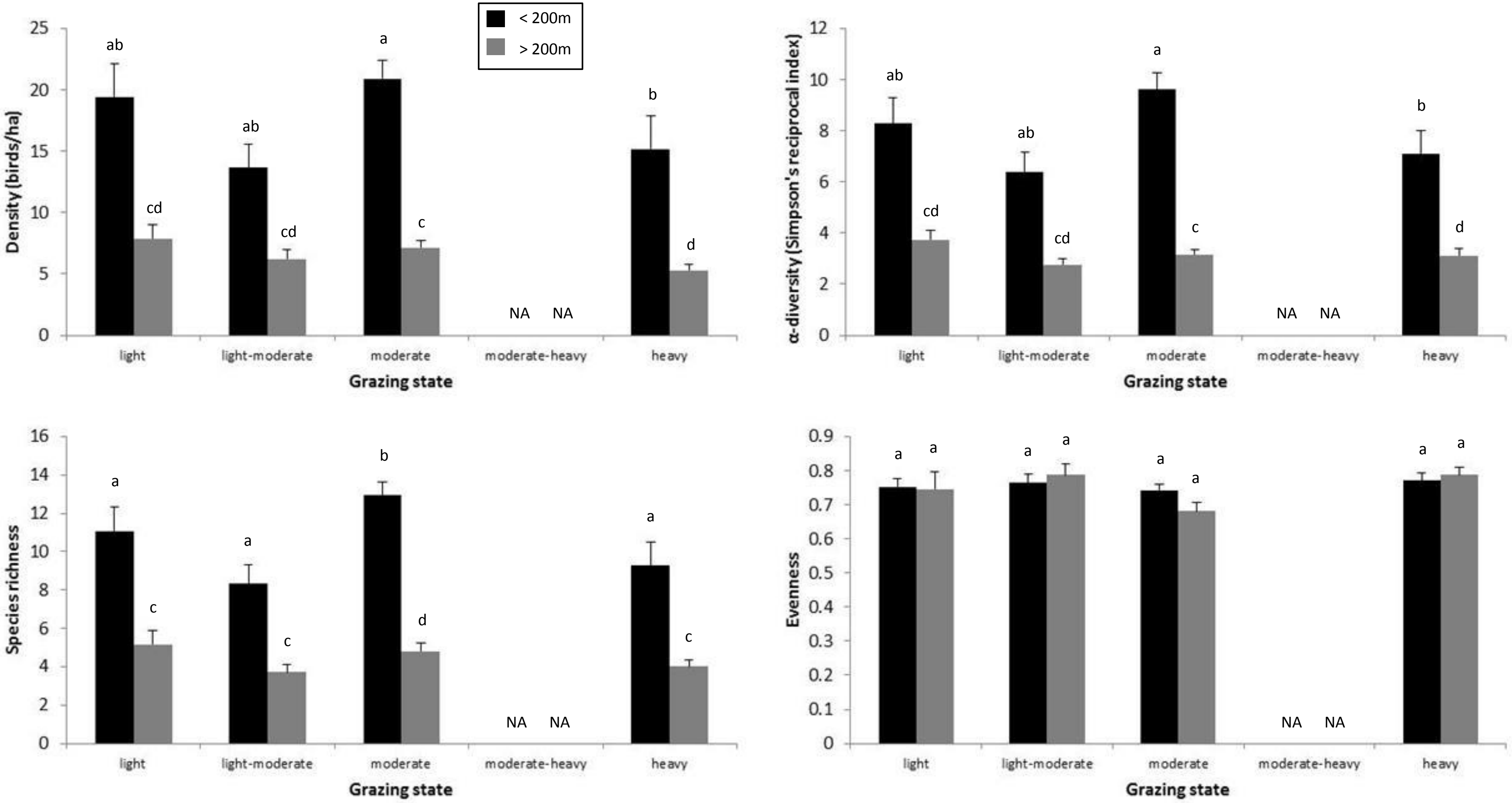


Fig. 4.2 Mean bird density, Simpson's alpha diversity, species richness and evenness across grazing state (2008).

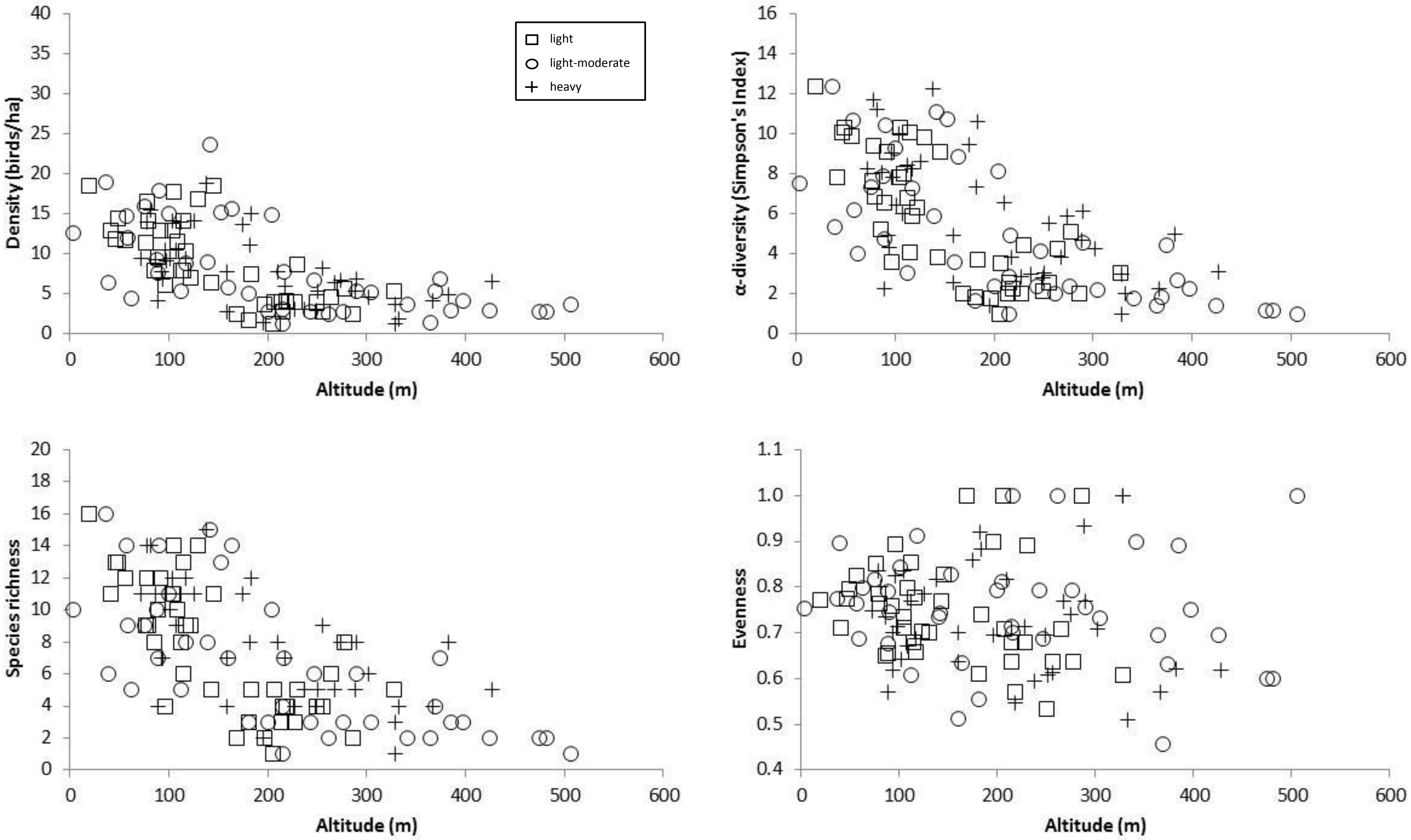


Fig. 4.3 Bird density, Simpson's alpha diversity, species richness and evenness across altitude (2007).

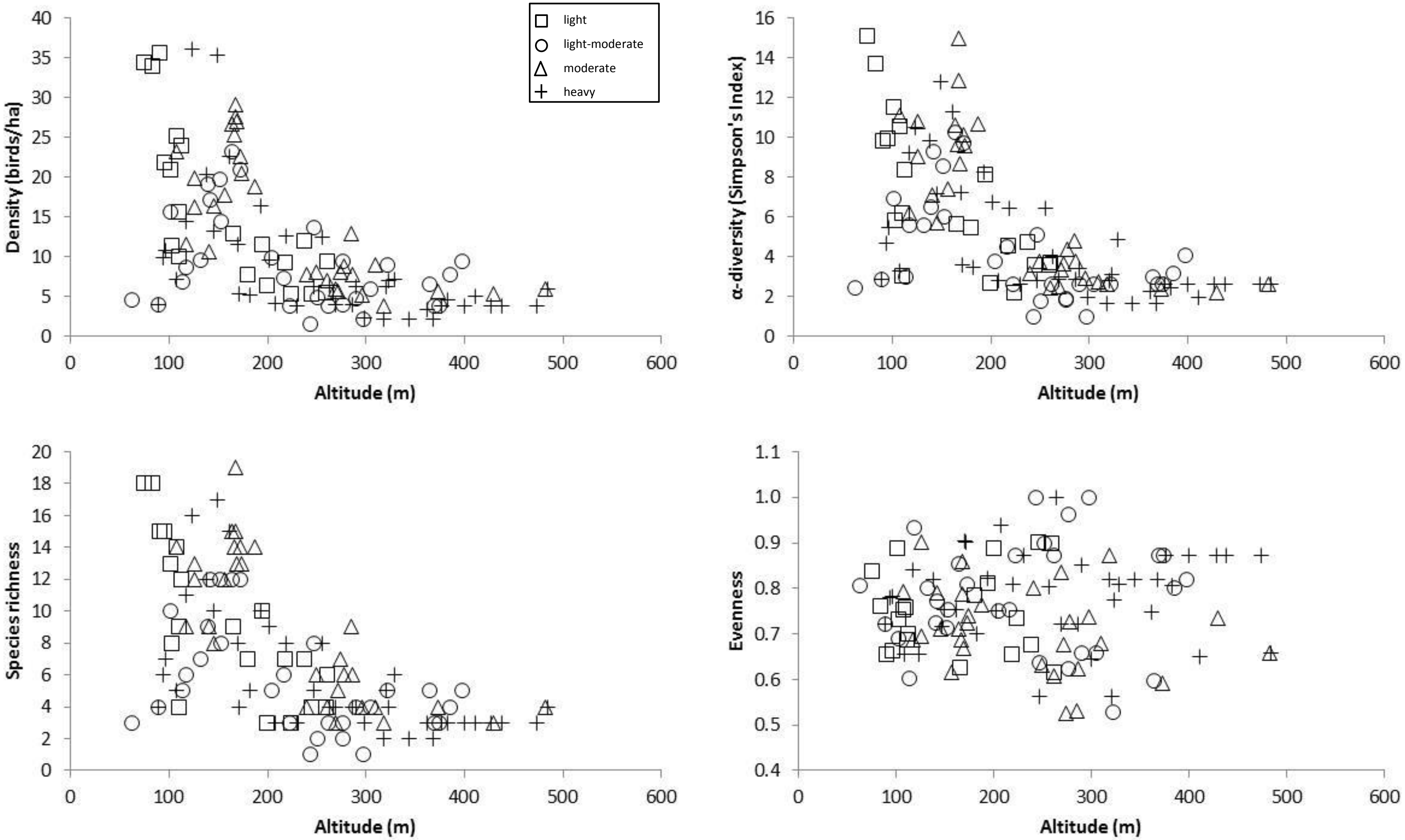


Fig. 4.4 Bird density, Simpson's alpha diversity, species richness and evenness across altitude (2008).

In 2008 there was no evidence to suggest an overall effect of grazing state on beta diversity ($F_{3,3}$: 4.06, $p = 0.140$). There was, however, a clear altitudinal effect ($F_{1,101}$: 10.44, $p < 0.01$), with higher similarity (and therefore lower beta diversity) in the uplands (estimate 0.297 ± s.e. 0.092). A significant interaction between grazing state and altitude (state : alt) ($F_{3,101}$: 4.16, $p < 0.01$) was also detected, which indicated greater similarity at higher elevations (therefore lower beta diversity), particularly on moderately grazed sites, as opposed to lightly-moderately grazed (estimate 0.334 ± s.e. 0.103) or heavily grazed (estimate 0.274 ± s.e. 0.097) sites. The steepest decline in beta diversity with an increase in elevation is observed in lightly grazed sites. A significant interaction was also found in beta diversity between % signs of grazing and % bare ground ($F_{1,101}$: 7.82, $p < 0.01$), with higher similarity (and therefore lower beta diversity) in heavily grazed areas with more bare ground (estimate 0.006 ± s.e. 0.002).

4.4.1.6 Regional (gamma) diversity

In the analysis of regional diversity (pooled bird species richness), an overall effect of grazing state was found in both 2007 ($F_{2,8}$: 11.785, $p < 0.01$) and 2008 ($F_{3,6}$: 25.366, $p < 0.01$) (**Fig. 4.6**). In 2007 regional diversity was significantly greater on lightly grazed state 1 than heavily grazed state 5 (estimate 1.882 ± s.e. 0.506), while lightly-moderately grazed state 2 contained greater regional diversity than state 5 (estimate 2.388 ± s.e. 0.391). Regional diversity in state 1 was considerably higher than in state 2 in 2008 (estimate -4.460 ± s.e. 0.697) or state 5 (estimate -4.455 ± s.e. 0.987). Moderately grazed state 3 had substantially higher regional diversity than either state 2 (estimate 3.393 ± s.e. 0.522) or state 5 (estimate 3.388 ± s.e. 0.563). % litter in 2007 ($F_{1,8}$: 18.231, $p < 0.01$) and % signs of grazing in 2008 ($F_{1,6}$: 6.827, $p < 0.05$) each had a positive effect on regional bird diversity.

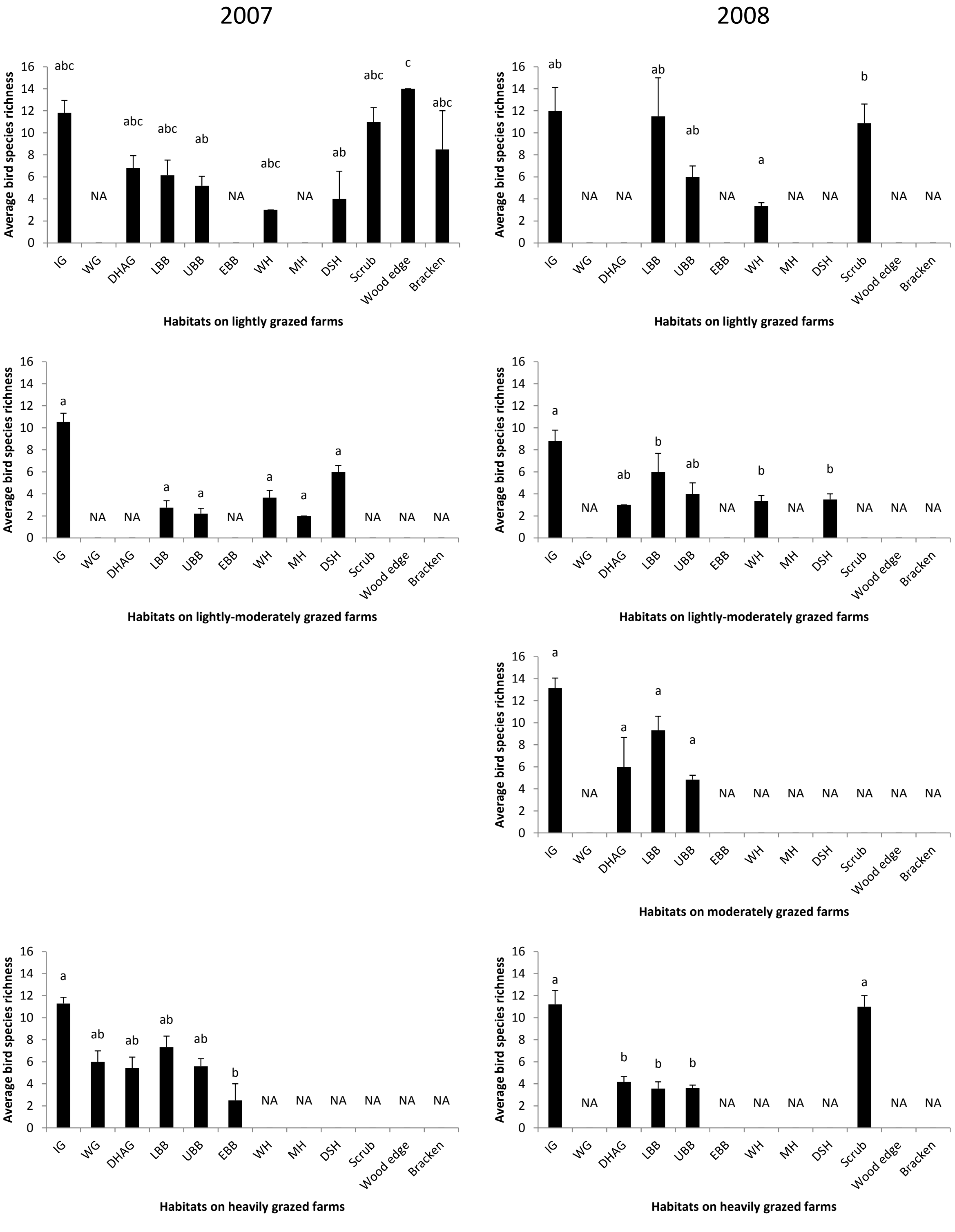
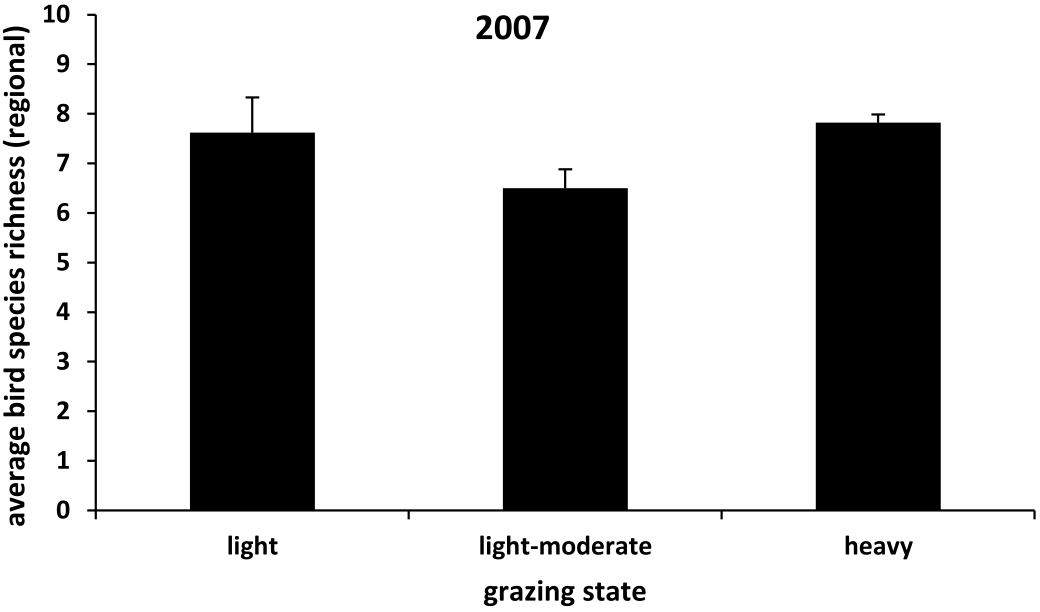


Fig. 4.5 Average bird species richness within grazing states, across habitats, in 2007 (left) and 2008 (right). IG = improved grassland, WG = wet grassland, DHAG = dry-humid acid grassland, LBB = lowland blanket bog, UBB = upland blanket bog, EBB = eroding blanket bog, WH = wet heath, MH = montane heath, DSH = dry siliceous heath.



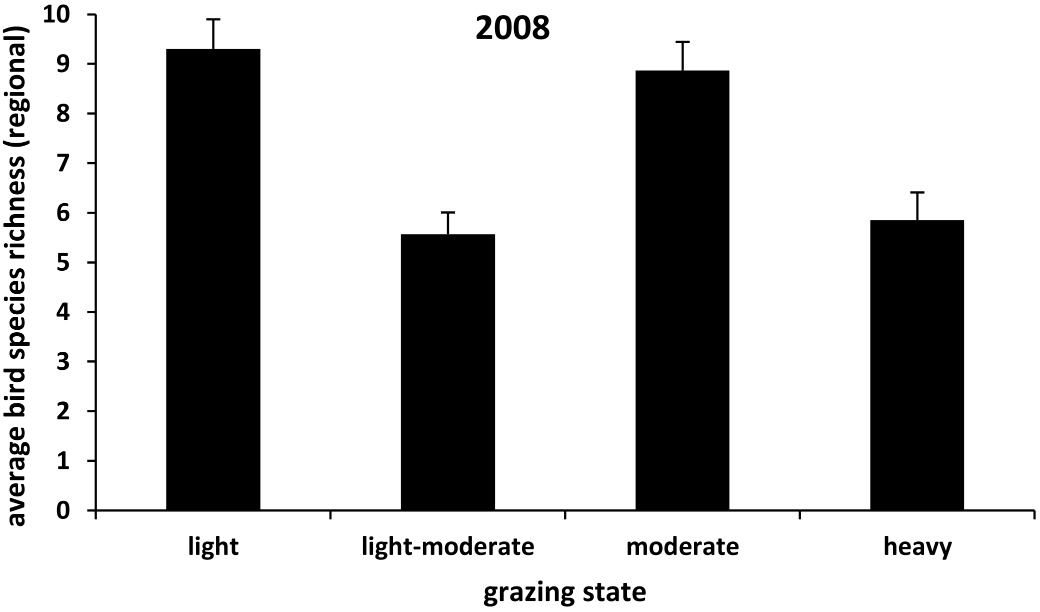


Fig. 4.6 Average bird species richness at the regional scale (gamma) across grazing states in 2007 and 2008.

4.5 Discussion

The present study investigated the way in which bird density, Simpson's alpha diversity, species richness, evenness, beta diversity and gamma diversity changed over a range of (i) grazing intensities, (ii) altitudes and (iii) habitats.

4.5.1 Grazing state effects

Although minor differences were observed, the results provided no evidence to suggest an overall effect of *grazing state* on bird density, Simpson's alpha diversity, species richness, evenness or beta diversity in 2007 or 2008 at the level of transect. Bird evenness exhibited the lowest variation between states. Previous studies have shown high levels of evenness in bird communities to be an indication of landscape fragmentation (Cushman and McGarigal, 2003), and perhaps this is one possible explanation as to why grazing states remain undetected in the present study. Grazing management, however, did appear to play a significant role in regional bird diversity, a finding supported by Bossenbroek *et al*. (2005). This may be explained firstly, by the fact that birds are highly mobile in nature and therefore factors such as farm management are only influential at the farm or regional scale. This is quite plausible, as farms are managed as individual units. Although birds cannot distinguish between different farms, they will be affected by changes in grazing management which alter the structure of their environment and therefore the ease at which they may acquire prey or avoid predation. It is recommended, in fact, that the response of a bird to the heterogeneous nature of its surroundings should be assessed at a large spatial scale (Benton *et al*., 2003). Secondly, grazing state may not affect birds at the local scale as a result of the farms in the present study falling at the lower end of the intensification scale. Other studies, however, have found local scale to be more important than large scale for birds (Fonderflick *et al*., 2010). Nevertheless the majority of studies recognise the value of sampling at several scales. Moreira *et al*. (2005) found that bird species richness was influenced by landscape, while abundance was affected to a greater extent by field management and more often depends on the ecology of each bird species (Batáry *et al*., 2007).

Although undergrazing was evident in many areas in the present study, true abandonment was scarce. At the other end of the scale, overgrazing was apparent, whilst, severe overgrazing was extremely difficult to find and even the most heavily grazed sites fell at the lower end of the intensity scale, with stocking rates never rising above 0.76 LU/ha. This would correspond with Brambilla *et al*. (2007), who found that because agricultural activities in their study areas were highly extensive and not heavily mechanised the highest farming intensity was relatively low from a European perspective. Perhaps over the gradient of grazing pressure documented here, an effect on the diversity of species with smaller ranges/distributions, such as plants or beetles, is more probable.

Nonetheless, there are several studies which have found that grazing management does affect bird diversity. While some investigations have discovered a negative effect of heavy grazing on birds (Fuller and Gough, 1999), others have found a positive effect (Loe *et al*., 2007). However, this varies with the metric under consideration (Báldi *et al*., 2005) and low bird density but high diversity was explained, in one study, by the contribution of farm buildings to the high landscape diversity. High levels of grazing are thought to be of particular benefit to insectivorous birds, especially those of smaller size, where the open habitat aids accessibility to prey (Söderström *et al*., 2001a; Vickery *et al*., 2001; Devereux *et al*., 2004; Atkinson *et al*., 2005; Evans *et al*., 2005; Vandenberghe *et al*., 2009). This concurs with Atkinson *et al.* (2004), who found that soil invertebrate feeders were positively influenced by heavy grazing pressure, while foliar invertebrate or seed feeders were negatively affected. Further analysis of data in the present study may detect this type of feeding group separation. Perhaps the higher than expected bird diversity on heavily grazed sites can be explained by the presence of soil invertebrate feeders. Ground nesting birds may be negatively affected by higher levels of grazing as a result of increased trampling, while lower levels of vegetation cover may also increase predation pressure (Vickery *et al*., 2001).

Abandoned land often supports greater species richness, although many of these species tend to be common. While the habitat heterogeneity created through extensive grazing is often important for many declining species (Verhulst, 2004; Woodhouse *et al*., 2005) and may, in fact, compensate for the loss of diversity in intensively managed sites (Tscharntke *et al*., 2005; Vallecillo *et al*., 2008) by creating a stabilising effect on bird communities (Devictor and Jiguet, 2007).

4.5.2 Altitudinal effects

In the present study bird density, Simpson's alpha diversity, species richness and beta diversity had a negative relationship with *altitude* over both years. This corresponds with previous work where bird abundance was also highest in the lowlands (Ratcliffe, 1990; Brown and Stillman, 1993). Altitude is often central in explaining bird species distributions (Debinski and Brussard, 1994) and may influence prey distribution (de los Santos *et al.*, 2002) as well as habitat features such as the presence of trees, hedgerows or buildings.

As found in this study, it is known that declines in bird species richness with elevation are common, however this will vary depending on the functional group (Terborgh, 1977) and peak species richness may not be found at the lowest elevation, it may be more reliant upon habitat heterogeneity (Finch, 1989; Vanhinsbergh and Chamberlain, 2001). Blake and Loiselle (2000) found that although species richness changed little below 1000m, compositional turnover (beta diversity) changed substantially along an elevation gradient in Costa Rica. However, the rate of species composition turnover with altitude, in the tropics, is known to be twice that of temperate regions (Jankowski *et al.*, 2009). Lennon *et al*. (2001) also found high species turnover in areas of low species richness, although it was scale dependent.

Previous work has found that grazing intensity is negatively correlated with elevation and has little effect on bird species at the highest altitudes, with the exception of skylark and linnet (Laiolo *et al.*, 2004). Bird species in the montane belt, however, have been shown to benefit from grazing management, although bird diversity was highest in areas subject to land abandonment. Here there was an increase in shrub-loving species and a corresponding displacement of open-habitat species to upland grasslands (Laiolo *et al.*, 2004). The key factor is that bird species associated with shrubland and trees tend to be fairly common generalists, while the majority of open-habitat grassland species are specialists with unfavourable conservation status. It is suggested that afforestation be avoided in areas with high open-habitat bird diversity (Henderson *et al.*, 2004; Laiolo *et al.*, 2004; Pithon *et al.*, 2005; Pollock *et al.*, 2005; Wilson *et al.*, 2012; Sirami *et al.*, 2007; Fonderflick *et al.*, 2010). The only significant interaction obtained between grazing state and altitude in the present study was in 2008 where Sørensen's similarity between grazing state and altitude was higher (lower beta diversity) on moderately grazed sites than on either lightly-moderately or heavily grazed sites. This may suggest that a moderate level of grazing results in lower species turnover but perhaps greater ecosystem stability. The largest difference in beta diversity between the uplands and lowlands was observed on lightly grazed sites. Perhaps the farms adopting lower levels of grazing management have tended to abandon grazing in their uplands, resulting in uniform vegetation structure, lack of habitat heterogeneity and substantially lower bird beta diversity.

4.5.3 Habitat effects

Although *habitat type* had an unsurprising significant effect on Simpson's alpha diversity and species richness in both years and on density in 2008 and beta diversity in 2007, *habitat diversity* appeared to play an insignificant role. Perhaps the gradient of habitat diversity within the present study farms was not sufficient to explain any variation present.

Improved grassland was frequently observed to contain significantly higher bird density, Simpson's alpha diversity and species richness than blanket bog, heath or acid grassland habitats. Boelscher (1988) also found variation in bird diversity between habitats, however, as in the present study, very little difference in evenness. Improved grassland also exhibited the highest species turnover rate of any habitat surveyed, a finding supported by Rotenberry and Wiens (1980) who showed that grassland sites had a higher bird species turnover than shrub dominated sites. There are several possible explanations for this. The first may simply be an altitudinal effect, as improved grassland was almost always found in the lowlands, where the highest bird diversity was also recorded. The second may be the result of large numbers of hedgerows and stone walls surrounding improved grassland fields, providing cover for many bird species. A final possible explanation may be related to the higher % dung produced as a result of higher stocking rates in the lowlands. This would have provided insectivorous birds with a plentiful supply of invertebrates. Scrub was also found to contain significantly higher bird density, Simpson's alpha diversity, species richness and beta diversity than blanket bog, heath or acid grassland habitats, as found in previous studies (Gillings *et al*., 2000; Vallecillo *et al*., 2008). Although scrub is known to have a negative impact on other taxa such as plants (Rosén and Bakker, 2005), it may provide birds with valuable cover from predators, as well as shelter from bad weather, while blanket bog or heath would generally be quite exposed. Scrub may also be a more stable habitat, with low species turnover which could provide microclimatic refuges during periods of environmental stress (Söderström *et al*., 2001b). However in the present study species turnover rate was high in scrub, suggesting that this habitat is merely a temporary stop for many species. This may be the case as previous studies have shown that no species are confined to scrub habitats alone (Fuller *et al*., 1999). Woodland edge was also an important habitat and contained higher species richness than blanket bog, heath or acid grassland. Nevertheless, even habitats low in species richness are still important areas for individual species such as the meadow pipit, when combined with other habitats into an optimum mosaic of heather, bog and grassland (Vanhinsbergh and Chamberlain, 2001). Others have also found that habitat heterogeneity has a positive effect on bird species richness (McMahon *et al*., 2008). Dry siliceous heath was found to contain significantly lower bird density, Simpson's alpha diversity and species richness than blanket bog, wet heath or acid grassland habitats. This, however, may have been due to dry siliceous heath only being recorded on lightly or lightly-moderately grazed farms.

Although there were no significant differences in bird species richness *between* grazing states in 2007, there were differences in bird species richness *within* grazing states, i.e. between the habitats of lightly grazed and heavily grazed states. There were no differences in bird species richness, however, between the habitats of lightly-moderately grazed states. This may reflect the differences in habitat composition between the grazing states. For instance lightly-moderately grazed farms have no dry-humid acid grassland habitats and lower bird species richness in both lowland and upland blanket bog. The habitats on lightly-moderately grazed farms may also be managed in a similar way, while those habitats of lightly or heavily grazed farms may not be, thereby implying that grazing state does have an impact on habitat type.

Although there were no overall differences in bird species richness *between* grazing states in 2008, as previously noted, moderately grazed states contained significantly greater bird species richness than lightly grazed, lightly-moderately grazed or heavily grazed states. No significant differences were found in bird species richness between the habitats *within* lightly or moderately grazed states. Therefore it is unlikely that habitat could explain the differences in bird species richness between these states and more likely to be accounted for by grazing management. Habitat may, however, explain the differences in bird species richness between moderately grazed and lightly-moderately grazed states and moderately grazed and heavily grazed states, as moderately grazed states have similar bird species richness across all habitats, while lightly-moderately grazed and heavily grazed states do not.

The fact that no significant difference in bird species richness was found *between* habitats *within* some grazing states may be explained by the higher than expected bird species richness in lowland blanket bog within those states. Improved grassland, dry-humid acid grassland and upland blanket bog were found across all grazing states and were home to similar numbers of bird species, suggesting that, here, habitat type was more important than grazing state. Lowland blanket bog was also found across all grazing states, however, there appears to be no consistent patterns in bird species richness within this habitat across grazing states or years, suggesting that in lowland blanket bog some other feature may be determining bird species richness, such as drainage, type and area of surrounding habitats, boundaries or vegetation structure, for example. It may also be possible that as lowland blanket bog was found across a wide range of altitudes, it is altitude which is having the largest effect on bird species richness in these habitats. Wet heath and dry siliceous heath were only found in lightly grazed and lightly-moderately grazed states, suggesting, again an influence of grazing management. Scrub was generally only found in lightly grazed states, with the exception of one heavily grazed farm which contained a large area of scrub between the improved grassland of the lowlands and upland blanket bog above 200m.

4.5.4 Structural, compositional and environmental factors

Sites exhibiting greater % grazing signs (bitten leaves) were found to contain higher bird beta and gamma diversity, while higher % bare ground resulted in lower bird density. Sites with larger % plant litter comprised higher bird alpha, beta and gamma diversity. This suggests that both overgrazing and undergrazing result in high bird species turnover. Farms containing high % forbs and plant species richness were found to have higher bird evenness but lower beta diversity. This suggests that habitats with high plant diversity, such as acid grasslands, may have a stabilising effect on birds (as found on moderately grazed sites), as evenness is high and species turnover low. Previous studies support this finding, concluding that forbs are a good indicator of grazing state, increasing in abundance with intermediate levels of grazing intensity (Dumont *et al*., 2009). However, other studies have shown that bird diversity is not related to plant diversity (Ralph, 1985). There appeared to be a soil moisture gradient from the drier grassland habitats, scrub and bracken to wet heath, upland blanket bog and water-logged lowland blanket bog. High % soil moisture was found on sites with lower bird beta diversity. Perhaps wetter soils or the presence of wet flushes may provide a greater abundance of invertebrates, many of which require water during their life cycle (Buchanan *et al*., 2006), which again provide a stable food resource for insectivorous bird species. Other studies have also shown that changes in bird species composition were correlated with moisture (Jankowski *et al*., 2009).

4.5.5 Management implications

Grazing by large herbivores can both positively and negatively affect ecosystem biodiversity (Côté *et al*., 2004) and several studies have shown that intensification and land abandonment can have both detrimental and beneficial effects on many species (Donald *et al*., 2001; Newton *et al*., 2004). Birds are valuable indicators of the effects of grazing management on biodiversity (Gregory *et al*., 2003). Although land abandonment has been shown to have negative consequences for biodiversity, such as the loss of preferred breeding sites for birds and the alteration of food supplies and predation pressure (Diáz *et al*., 1997; Suárez *et al*., 1997; Fuller and Gough, 1999; MacDonald *et al*., 2000; Suárez-Seoane *et al*., 2002), some studies show that abandonment may not necessarily result in an overall decrease in biodiversity, rather, a decrease in those birds that are rare or threatened (Verhulst *et al*., 2004). Landscape type is crucial in determining the effect of land abandonment on bird species. The initial stages of abandonment lead to an impoverishment of the bird communities as typical open habitat species decline. As the scrub matures, however, a temporary rise in species numbers occurs as woodland generalists and shrubland species appear alongside farmland generalists. With the maturation of the woodland, the bird community is eventually simplified as it becomes dominated by woodland specialists and shrubland and ecotone species are lost (Sirami *et al*., 2008). There is evidence to suggest that land abandonment benefits birds associated with scrub and woodland at the detriment of open habitat species (Preiss *et al*., 1997; MacDonald *et al*., 2000; Suárez-Seoane *et al*., 2002; Verhulst *et al*., 2004; Vallecillo *et al*., 2008), however this appears to vary with successional stage (Sirami *et al*., 2008). In many cases it requires a trade-off between agricultural intensification and long-term abandonment (Brambilla *et al*., 2007). An intermediate level of grazing should maintain the mosaic of habitats and heterogeneous vegetation structure required by as many species as possible. The inclusion of approximately 15 % scrubland, wherever achievable, is recommended (Nikolov, 2010). The % scrub cover on farms in the present study ranged from 0 – 29 %.

Although little evidence was found in the current investigation to suggest an overall effect of grazing state on bird density, Simpson's alpha diversity, species richness, evenness or beta diversity, some factors such as % signs of grazing, % bare ground and % vegetation litter provided evidence of a local effect of grazing management. There was also a clear influence of grazing state on regional diversity. Nonetheless, it was altitude and habitat which stood out as the principal factors affecting all five transect-scale bird measures.

By concentrating on the diversity of a community, there is a risk of oversimplification, and consequently the loss of information (Cole *et al.*, 2006). Functional traits may help predict species responses to land use change and facilitate the understanding of ecosystem properties on both a short and long time scale (Pakeman, 2004; Quétier *et al.*, 2007; Pakeman and Marriott, 2010) as well as removing the reliance on key indicator species (Cole *et al.*, 2002). Insectivorous birds, for example, are strongly affected by the seasonality of their food supply and would perhaps be influenced by grazing management to a greater extent than other functional groups such as granivores (Söderström *et al.*, 2001a; Buckingham *et al*, 2004; Douglas *et al.*, 2008), as some studies have shown (Cole *et al.*, 2006; Dennis *et al.*, 2008).

The way in which spatial and temporal scales, (Edwards, 2005) influence upland farming systems are crucial when seeking to understand the nature of the response of a species to change. Birds select habitats differing in structure, quality and management at both the local and landscape scale (Milne, 1996; Suárez-Seoane *et al.*, 2002; Atkinson *et al.*, 2004; Fuller *et al.*, 2004; McCracken and Tallowin, 2004; Tews *et al.*, 2004; Oom *et al.*, 2008; Perlut et al., 2008). Regional scale processes, as shown in this study, are especially important for highly mobile species such as birds (Tucker, 1997; McCracken and Bignal, 1998; Söderström *et al.*, 2001b; Báldi *et al.*, 2005; Reif *et al.*, 2008). The multi-scale approach is also critical when studying species-habitat relationships on different trophic levels (Pearman, 2002; Tscharntke *et al.*, 2005).

Climate will also influence grazing management and heavy rainfall may exacerbate any impacts of over-stocking on the vegetation (Söderström *et al.*, 2001a), especially in habitats such as blanket bog. Milder, wetter springs and summers, as a result of climate change, may lead to a decrease in specialist alpine bird species and a corresponding increase in generalists (Thompson *et al.*, 2012). Cold temperatures are a particular problem for smaller bird species such as the wren, for example, whose population numbers may fluctuate substantially after a particularly warm or cold winter (Lysaght, 1989). Season is also important and concentrated grazing at certain times of the year will certainly encourage different bird species during these periods (Durant *et al*., 2008). Mixed sheep and cattle summer grazing has been shown to reduce the tough and unpalatable grass, *Nardus stricta* in the drier upland grasslands (Dennis *et al*., 1997). However in the Burren, in Ireland, winter grazing is shown to promote biodiversity and prevent scrub encroachment (Dunford, 2002). Other studies have shown that in summer many bird species have a negative relationship with sward height, and, in winter, a positive relationship with bare ground (Atkinson *et al*., 2004). Previous work has shown that if stocking rates remain static throughout the year a site may become overgrazed in the winter and undergrazed in the summer (Ebrahimi *et al*., 2010).

4.6 Conclusions

Half of all European farmland bird species have been lost over the last 25 years and many are still in decline, particularly specialists such as skylarks (Gregory *et al*., 2004; Gregory *et al*., 2005; PECBMS, 2009; Copland *et al*., 2012). Populations of upland bird species have also fallen sharply (Eaton *et al*., 2010), making studies such as this of significant importance.

The pattern of decline in skylarks in lowland agricultural habitats is different from that in upland landscapes, implying a different cause (Chamberlain and Crick 1999). The decline in skylarks in the uplands may be attributed to a greater increase in sheep numbers in the uplands (Fuller and Gough 1999). As upland birds tend to move to the lowlands in the winter, there is a possibility that lowland agricultural changes, however, are also influencing upland populations (Chamberlain *et al*., 1999).

The key findings in the present study demonstrated the lack of significant impact of grazing management on bird diversity at the local scale, while differences in regional diversity were detected. Habitat diversity appeared to have had little effect, while habitat type was fundamental and the importance of altitude, definitive. Scrubland habitat was of particular importance, suggesting that a degree of land abandonment may be beneficial for birds. This is supported by the fact that bird density, in the present study, increased until the % scrub per farm reached 16 %, after which it began to decline again. Bird diversity, however, was not affected. Therefore, the high levels of bird diversity are more likely a reflection on the presence of habitat mosaics, rather than solely on scrub occurrence.

The major challenge is to balance biodiversity with livestock production. An understanding of bird species responses to grazing management in the uplands is vital in preventing the negative effects of CAP reform, and as birds are valuable indicators of the health of a system, similar studies will also inform on wider ecosystem function and diversity. Some would argue that it will be impossible to attain a range of habitats at the correct grazing levels to fulfil the requirements of a maximum number of species and taxa (Milne, 1996; Holland *et al.*, 2010). Perhaps then, the focus should fall on maintaining the maximum number of functional traits. Another option may be to allocate priority to sites with specific designations, large areas containing the feature of interest or areas of both local and national importance (Cooper *et al.*, 2007; Holland *et al.*, 2010). It is possible that with the recent economic downturn (2010-2012), and consequent losses in the construction industry, which provided supplementary income to many farmers, there may be a renewed increase in hill farming.

Irrespective of the method adopted, it is essential that social, economic and ecological factors are considered alongside one another, and species-rich farmland is not maintained simply by the promotion of rural poverty (McCracken *et al.*, 1997). The landscape must be regarded as an integral unit, regardless of ownership or past management practices (Cobb *et al.*, 1999). The key link between policy and conservation management of upland areas is grazing pressure (Hanley *et al.*, 2008) and the successful use of grazing management for biodiversity enhancement lies in site-specific planning in conjunction with local conditions, residents and land managers (Brown and Stillman, 1993; Marriott *et al.*, 2004; Edwards, 2005; Metera *et al.*, 2010).

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Chapter 5

The influence of upland grazing management on breeding bird assemblages

Roslyn M. Anderson, Mark C. Emmerson, Mark W. Wilson and John O'Halloran

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Raven (*Corvus corax*) on grazed hillside (Photo: Roz Anderson).

5.1 Abstract

Agricultural subsidies throughout Europe have seen the intensification of the lowlands and abandonment of the uplands. As one of the prominent forms of land use across much of upland Europe, hill sheep farming holds the key to the sustainable management of these landscapes for the benefit of many species. Very little is known about upland bird species composition in Ireland, therefore populations of birds were sampled on 21 farms in County Kerry in the southwest of Ireland over the breeding seasons of 2007 and 2008. Study farms represented a grazing continuum of lightly to heavily grazed states. DISTANCE software was used to estimate bird densities. Non-metric multidimensional scaling (NMS) ordination was used to determine which management and environmental factors were most influential in explaining bird community composition. Bird species assemblage was influenced to the greatest extent by altitude (almost 75% variation), as were individual species. Grazing state and other management variables explained around a third of the variation in community composition, while habitats such as scrub and improved grassland were also important. Functional feeding groups such as ground or foliage insectivores (birds dependent upon invertebrates), or granivores were influenced by grazing management to a small extent. It is clear that environmental factors such as altitude and habitat play a key role in explaining bird assemblage composition and structure. The uplands, and particularly the habitats found at higher altitudes, are very important for bird species such as meadow pipit (*Anthus pratensis*) and skylark (*Alauda arvensis*). Nevertheless, grazing management is also fundamental as a means of preventing the loss of open habitats vital to so many species of conservation concern.

5.2 Introduction

Many of Europe's agricultural landscapes are over 2000 years old (Kleijn *et al*., 2006). In the uplands of Britain and Ireland centuries of deforestation and the subsequent establishment of managed grazing has led to the creation of semi-natural landscapes. Grazing by sheep (*Ovis aries*), cattle (*Bos taurus*), goats (*Capra hircus*) and native deer have maintained these open areas (Ratcliffe and Thompson, 1988; Usher and Gardner, 1988; Ratcliffe, 1990; Averis *et al*., 2004) leading to the coevolution of associated species over time (Kleijn *et al*., 2006). The present study is focused on quantifying the effects of grazing management and environmental gradients on bird species assemblages in the uplands.

There is no clear definition separating the ‘uplands’ from the ‘lowlands’ (Ratcliffe and Thompson, 1988; Usher and Gardner, 1988), although, definitions of uplands, such as those areas lying ‘typically above the limits of enclosed farmland’ or altitudes above 200m (Ratcliffe and Thompson, 1988; Milne, 1996; Thompson *et al*., 1995) are very similar to the definition of mountains by the European Commission Council Regulation 1257/99 (Article 18). Körner *et al*. (2011) argue that a mountain cannot be defined by elevation alone and that ruggedness or steepness is a better descriptor, with the use of thermal belts to partition biodiversity. Using this definition they have estimated that 12.3% of the world’s terrestrial land area outside Antarctica is mountainous. Others define the uplands as land within ‘Less Favoured Areas’ which includes lower hill country, enclosed hill farmland and mountains (House of Commons - EFRACOM, 2011). Others use habitat or environment to define the uplands, such as those areas composed of predominantly dwarf shrub heaths, grasslands and peat bogs (Pearsall, 1950; Ratcliffe and Thompson, 1988; Averis *et al*., 2004). It is estimated that about 30% of Britain and about 25% of Ireland is upland (Ratcliffe and Thompson, 1988; Ratcliffe, 1990).

The Common Agricultural Policy (CAP) is amongst the most important land use policies within the EU. Through production subsidies implemented under the CAP, livestock numbers increased substantially over many decades. This resulted in countless areas becoming severely overgrazed (Bleasdale, 1998; Midmore *et al*., 1998; Caraveli, 2000). However, the recent decoupling of these subsidies from production, in the form of environment and rural development support has introduced new concerns over undergrazing and land abandonment (MacDonald *et al*., 2000; Acs *et al*., 2010). Whilst production subsidies have led to an intensification of lowland agriculture, there has been little pressure on the uplands. Recent declines in sheep stocking densities in upland areas have heightened this divide, with many upland areas becoming completely abandoned (Caraveli, 2000; Averis *et al*., 2004; Matthews *et al*., 2006).

It is the agricultural intensification in some regions and simultaneous abandonment of others which remains a major threat to the ecology of agro-ecosystems (Stoate *et al*., 2009). Intensification, through high levels of grazing and trampling, fertilizer application, mowing and an increase in field size, has led to decreased plant diversity and decreased habitat complexity, with remaining habitats dominated by competitive species and lower invertebrate and bird numbers (Vickery *et al*., 2001; Benton *et al*., 2002; Atkinson *et al*., 2004).

Farmland bird conservation is under threat worldwide (Hanspach *et al*., 2011), with approximately one third of all bird species of conservation concern in Europe utilizing agricultural grasslands (Perkins *et al*., 2000). Pastoral habitats are known to have suffered more local bird extinctions than arable areas (Atkinson *et al*., 2004). In the uplands the majority of British and Irish bird species are not scarce, however, the characteristic bird assemblages of these areas are distinctive, consisting of a greater mixture of boreal, low-, mid- and high-arctic, temperate and continental species than in any other comparatively sized part of Europe (Ratcliffe and Thompson, 1988).

Birds, in particular, have been found to respond to the effects of grazing (Milchunas *et al*., 1998). Overgrazing, specifically by sheep, has led to the loss of preferred vegetation types, the deterioration of the sward for nesting, the alteration of predation pressure, the modification of food supply, such as seed resources or invertebrate prey (Fuller and Gough, 1999; Vickery *et al*., 2001) and in some instances, soil erosion, although it is debatable whether overgrazing alone leads to soil erosion (Rowentree *et al*., 2004). At the opposite end of the spectrum, the complete exclusion of livestock has also been shown to reduce bird density and species richness (Garcia *et al*., 2008). The disruption of food chains may in fact lead to a reduction in the overall numbers of species in an ecosystem (Stoate *et al*., 2001). Heavy grazing on previously wooded areas often results in large areas of bracken growth (Ratcliffe and Thompson, 1988). In small patches both bracken and scrub may be beneficial for bird species, and in fact some suggest that the large-scale regeneration of scrub and woodland can maximise bird diversity (Fuller *et al*., 1999; Gillings *et al*., 2000). Scrub encroachment, however, may also be regarded as a type of fragmentation that can be detrimental to open habitat bird species (Coppedge *et al*., 2001; Laiolo *et al*., 2004), favouring more common and widespread species (Stoate *et al*., 2001). Alternatively, an adequate level of grazing may create an open, patchy sward, while the deposition of dung will create localised sources of invertebrates, which will increase the availability of prey for insectivorous birds (Tucker, 1992; Wilson *et al*., 1996; Atkinson *et al*., 2005), as well as undigested grains for granivores (Yuan, 1996) and create conditions suitable for a wide variety of plant and animal species (Pykälä, 2005).

The uplands of Britain and Ireland have particular international significance owing to their unique hyper-oceanic climates (Ratcliffe and Thompson, 1988). Biogeographical and evolutionary constraints have limited bird species richness in Ireland, defining a unique Irish avifauna composition (Kelly, 2008). Over 17% of Ireland's land area is peatland, the third largest in Europe. Undamaged, this is one of the few remaining pristine ecosystems in the world, as well as a valuable carbon store (Gorham, 1991; Clymo *et al*., 1998; Bracken *et al*., 2008; Connolly and Holden, 2009; CORINE 2006-EPA/EEA, 2009; Connolly *et al*., 2011). Peatlands are considered priority habitats under Annex 1 of the European Union Habitats Directive (92/43/EEC) (Crowley *et al*., 2003). They are important habitats for bird communities, particularly meadow pipit and skylark, however few studies exist on the birds of peatland (Bracken *et al*., 2008) or the uplands of Ireland (O'Halloran *et al*., 1993; Smiddy *et al*., 1995; Henderson *et al*., 2002; Wilson *et al*., 2009). Although there has been some research into bird communities of Irish farmland, it has generally focused on the more diverse lowlands (Lysaght, 1989; Moles and Breen, 1995; Taylor and O'Halloran, 2002; Pithon *et al*., 2005; Bracken and Bolger, 2006; McMahon *et al*., 2008; 2010a; 2010b). Only one other study has quantified the effects of grazing on birds on upland bogs in Ireland (Watson and O'Hare, 1979).

Here we investigate how the bird assemblages of hill sheep farms are influenced by both management and environmental factors. In particular four questions are addressed: (i) How do bird assemblages vary among lightly, moderately and heavily grazed farms? (ii) In what way do bird assemblages change with altitude? (iii) What habitat and vegetation characteristics are most influential in explaining observed patterns in bird assemblages? And (iv) In what way are functional groups and individual species affected by grazing, altitude and habitat?

5.3 Methods

5.3.1 Study area

The study was conducted on the Iveragh Peninsula (51° 94´ N, 9° 89´ W) in County Kerry, southwest Ireland. A high annual rainfall and nutrient deficient soils combine to produce the blanket bogs and heaths which characterise the area (Carruthers, 1998; Averis *et al*., 2004; Crowley and Sheehan, 2009). The majority of the peninsula's 1400km^2 consists of upland marginal land (O'Rourke and Kramm, 2009), often suitable only for sheep farming. Seven geographically distinct study areas within Iveragh were selected as being representative of upland grazing conditions on the peninsula as a whole. Within each of these study areas, three hill farms subject to grazing regimes of varying intensity were chosen. Farmland generally extended between altitudes of 400m and 800m, although total farm areas were normally less than 250ha. Sheep stocking rates ranged from 0.06 – 0.76 LU/ha over the whole farm and 0.005 – 0.48 LU/ha in the uplands.

5.3.2 Grazing state classification

Following an initial visit, all farm habitats were mapped (Fossitt, 2000; Hill *et al*., 2005). Each farm generally consisted of a heterogeneous mosaic of grazing intensities and habitats. The impacts of grazing, browsing and trampling by large herbivores in upland habitats were quantified by adopting the standard methodology of MacDonald *et al*. (1998). Habitat-specific field indicators such as the directly observable, accumulation of dead plant material (litter), cover of bare ground, selectivity of grazing and presence of dung, were employed. Light, moderate and heavy (L, M and H, respectively) impact categories were then used to evaluate alternative states for each field indicator, using a number of point estimates or quadrats, and an overall estimation for a particular habitat type was thus derived.

To account for spatial heterogeneity, the percentage of the area occupied by each impact class was calculated in order to summarise the impact across a habitat (Agresti, 1984; Brewer *et al*., 2004; Albon *et al*., 2007). The three class impact scale was therefore smoothed into a more continuous five point scale by the introduction of intermediate classes light/moderate (L/M) and moderate/heavy (M/H) (after Albon *et al*. 2007). Similar systems such as the allocation of weightings to each L, M or H indicator to generate a numerical sum for each surveyed area have also been adopted (O'Hanrahan, 2005). Previous studies have likewise used livestock units as a measure of grazing intensity (Pain *et al*., 1997), however, using indicator variables is more useful as the same number of stock can have different impacts if the productivity is different (Meg Pollock, pers. comm.).

In total, 144 2m x 2m quadrats were sampled on twelve farms in 2007 and a further 108 quadrats from an additional nine farms in 2008. Structural, environmental and plant explanatory variables such as vegetation height (cm), soil depth, soil pH, soil moisture and plant species richness (133 plant species were recorded in total using Braun-Blanquet percentage cover estimates), were analysed in conjunction with the 2007 bird survey data.

ArcGIS 9 (2008) was used to digitise habitat maps for each farm, which allowed the calculation of variables such as habitat diversity (Shannon-Wiener Index) and altitude. The habitat maps also enabled the association of habitat type with each bird transect, as well as the estimation of percentage cover and total area of each habitat per farm (Gregory and Baillie, 1998).

5.3.3 Bird surveys

Breeding birds were recorded on two dates separated by at least a month (from April-June 2007 and 2008). The first farm visit recorded resident birds and the second incorporated migrant species later in each year. Through the integration of the methodologies of the Breeding Bird Survey (Newson *et al.*, 2009) and the Countryside Bird Survey (Coombes *et al.*, 2006; Crowe *et al.*, 2010) and Bibby *et al.* (1992), an approach specific to this study was implemented.

Two 1km transects were surveyed, one below 200m in altitude and one above 200m, situated about 500m apart. Counts began an hour after sunrise to avoid the dawn peak in bird activity but were not undertaken in conditions of rain or strong winds (Herzon and O'Hara, 2007). For each transect the maximum count of individuals per species from the two visits was used (Brown and Stillman, 1993; Browne *et al.*, 2000; Pearce-Higgins and Grant, 2006; Herzon and O'Hara, 2007). The sequence in which transects were surveyed was reversed between visits in order to minimise any bias in time of day surveyed.

All birds seen and/or heard along transects were recorded in distance categories (within 25m, between 25 and 100m and between 100 and 300m) perpendicular to the central transect line (Vanhinsbergh and Chamberlain, 2001). Actual distances were only recorded in 2008. Data gathered in 2007 were assigned an average distance, corresponding to the mid-point of each distance class, so that Group 1 was 12.5m, Group 2 was 63m and Group 3 was 200.5m. Distance sampling software (Buckland *et al.*, 1993; DISTANCE Version 5) was used to estimate bird densities (number of individuals per hectare). To account for any inter-annual variation, but to maximise the size of the study area, three farms from 2007 (one from each of the MacDonald *et al.*, 1998 classified grazing states) were again surveyed in 2008.

5.3.3.1 General observations

General observations noted the presence of a core group of species across all grazing states: meadow pipit, wren, chaffinch, dunnock, blackbird, robin and swallow. Stonechat and linnet were generally only recorded in lightly or lightly-moderately grazed states, while starling and pied wagtail were most common in heavily grazed states.

All habitats shared the same core group of species: meadow pipit, wren, chaffinch and dunnock. The greatest number of species was found on improved grassland, lowland blanket bog and scrub. The highest number of insectivores and granivores were found on improved grassland, which also contained the greatest number of species of conservation concern, followed by lowland blanket bog, then scrub. A few species did appear to favour some habitats over others. Snipe, for example, were only found on lowland blanket bog, while starling and pied wagtail were only recorded on improved grassland. A high percentage of upland blanket bog on a farm was linked to low habitat diversity but also high meadow pipit density in the uplands. Farms containing higher percentages of upland blanket bog were found to have lower densities of species such as wren, dunnock (*Prunella modularis*) and stonechat, which require the drier scrub or acid grassland habitats.

5.3.4 Data analysis

Non-metric multidimensional scaling (NMS) was used to analyse bird species composition and densities (Sweeney *et al*., 2010a; 2010b), in relation to management and environmental variables across transects, using PC-Ord 5 (McCune and Mefford, 1997). NMS is an ordination method well suited to data that are non-normal or which lie on an arbitrary scale (McCune and Grace, 2002) and was chosen over the more traditional eigenanalysis techniques such as PCA, DCA or CCA, as it has been found to be better at recovering complex gradients (Wilson *et al*., 2006) and does not require data transformation (Clark, 1993). Given these issues it has been proposed as the most appropriate ordination method for ecological data (Kenkel and Orlóci, 1986; Clark, 1993; McCune and Grace, 2002).

NMS makes an iterative search for the position of bird species densities and environmental variables on *k* dimensions (axes) which give rise to the lowest stress based on ranked similarity distances (Acevedo and Aide, 2008; Acevedo and Restrepo, 2008). A random starting configuration with a maximum of six axes, a stability criterion of 0.0005, 50 permutations with real data, 20 iterations to evaluate stability; a maximum number of iterations of 500; an initial stepdown of 0.2 and 50 randomised permutations for Monte Carlo testing were selected. Sørensen distance measures were used. All species occurring in less than 5% of transects in an ordination were excluded. Results were selected on the basis of those NMS plots and solutions which had a minimum number of dimensions and the lowest stress and instability values (McCune and Grace, 2002). Relationships between ordination axes and environmental variables were investigated using Spearman's rank correlations, using SPSS 16.0 (2007) (Wilson *et al*., 2006).

For multiple comparisons across conservation status groups and feeding groups, the non-parametric Kruskal–Wallis test was performed, followed by a post-hoc Kruskal–Wallis procedure (Papanikolaou *et al*., 2011), using the pgirmess R package.

5.4 Results

A total of 56 species (3806 individual maximum bird counts) were recorded over two breeding seasons in 2007 and 2008. Of these, 48 species were used in the analysis, as eight species occurred in less than 5% of the sites.

5.4.1 Grazing state

The Kruskal-Wallis multiple comparison tests highlighted the greater number of bird species in the present study with a green conservation status ($P < 0.0001$) in both years (**Fig. 5.1**). The lowest number of species was consistently found on the lightly-moderately grazed sites in both 2007 and 2008. Interestingly, however, the lightly-moderately grazed sites also supported species of conservation concern, such as the Red Grouse (*Lagopus lagopus scotica*), a subspecies endemic to Britain and Ireland (Fuller *et al*., 1999). Nevertheless, it was the heavily grazed sites which contained the highest number of species on the amber list. Fifteen species of conservation concern in total (i.e. either red or amber listed, as classified by Newton *et al*., 1999; Lynas *et al*., 2007) were recorded (**Table 5.1**).

There were significantly more insectivore species recorded than granivores, omnivores or scavengers ($P < 0.0001$) in 2007 and 2008 (**Fig. 5.1**). There is a preference by insectivores (**Table 5.1**) for heavily grazed sites, which may explain the higher numbers of ground feeding insectivores recorded on these sites, while the lightly grazed farms had higher numbers of foliage invertebrate feeders. Granivores were more commonly found on moderately grazed sites, while scavengers were found in equal numbers across all grazing states.

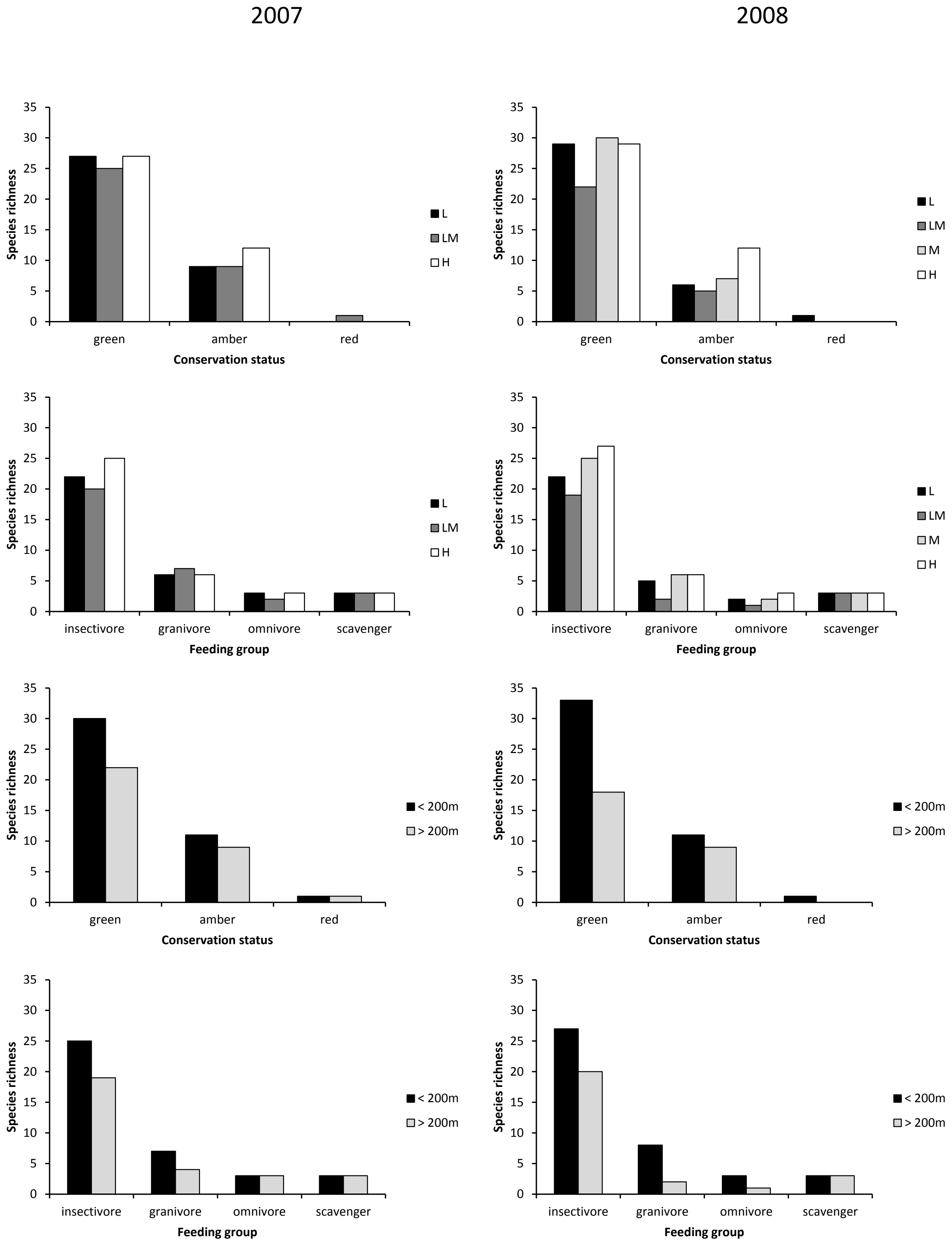

Fig. 5.1 Total species richness of breeding birds across conservation status groups (green, amber and red) and feeding groups (insectivores, granivores, omnivores and scavengers) in 2007 and 2008. Data has been separated into grazing categories (L = light, LM= light-moderate, M = moderate and H = heavy) and altitudinal categories (< 200m and > 200m) for comparisons.

5.4.2 Altitude

The greatest number of species was found in the lowlands, as were the majority of insectivores and granivores (**Fig 5.1**). Granivores are thought to be mainly affected by habitat type and grazing state, as a result of their highly selective feeding behaviour (Marone *et al.*, 2008). Scavengers, however, were equally abundant in the uplands and lowlands. The number of species of conservation concern in the uplands was consistent over both years, however, many more species of conservation concern were found in the lowlands in 2007 than in 2008. This suggests that site specificity may play a large role in presence of declining or threatened species.

5.4.3 Species densities

Average bird density per farm was found to increase as % scrub increased (**Fig. 5.2**). However, no effect was found on average bird diversity, species richness or evenness. % scrub per farm ranged from 0 – 29%.

The average density of all birds across farms in 2007 was 111 individuals per km^2 and 160.1 individuals per km^2 in 2008. There was a general decline in bird density moving from lightly grazed to heavily grazed farms. Density was also higher in the lowlands and in scrub, wet heath and improved grassland. Average meadow pipit density over all farms was 120.2 individuals per km^2 in 2007 and 193.7 individuals per km^2 in 2008. Meadow pipit density in the uplands was almost twice that in the lowlands and moderately grazed sites saw the highest meadow pipit density, while, contrary to overall bird density, meadow pipit were found at highest densities on blanket bog. Average skylark density over all farms in 2007 was 16.1 individuals per km^2 and 37.5 individuals per km^2 in 2008. In 2007, as expected, skylark density was highest on the most heavily grazed farms, however in 2008 lightly and moderately grazed farms contained higher skylark density. As with meadow pipit, skylark density in the uplands was almost twice that of the lowlands and blanket bog contained the highest density. Average wren density over all farms in 2007 was 129.4 individuals per km^2 and 185.4 individuals per km^2 in 2008. As predicted, wren density declined as one moved from lightly to heavily grazed farms and density was one and a half times higher in the lowlands than in the uplands. Scrub contained the highest wren density of all habitats, closely followed by improved grassland and heath.

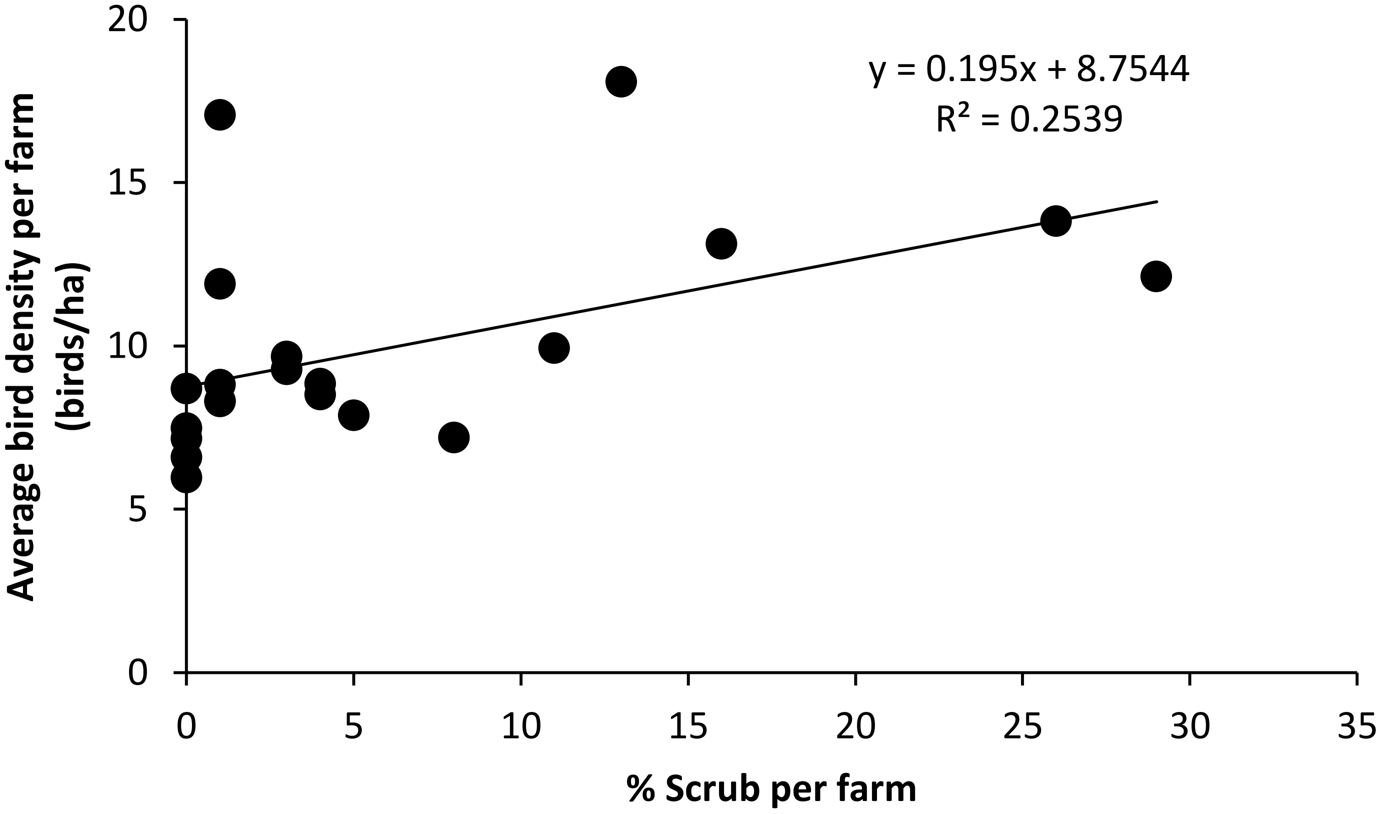

Fig. 5.2 Showing significant relationship between average bird density over all 21 farms in the present study against total % scrub on each farm.

Table 5.1 Bird species and functional feeding group categories.

Bird species	code	Latin name	Functional group	Conservation status
Blackbird	B.	*Turdus merula*	Insectivore (ground)	Green
Blue Tit	BT	*Cyanistes caeruleus*	Insectivore (foliage)	Green
Chiff-Chaff	CC	*Phylloscopus collybita*	Insectivore	Green
Chough	CF	*Pyrrhocorax pyrrhocorax*	Insectivore (ground)	Amber
Coal Tit	CT	*Periparus ater*	Insectivore (foliage)	Green
Common Sandpiper	CS	*Actitis hypoleucos*	Insectivore	Amber
Cuckoo	CK	*Cuculus canorus*	Insectivore (foliage)	Green (Red in UK)
Dunnock	D.	*Prunella modularis*	Insectivore (ground)	Green (Amber in UK)
Goldcrest	GC	*Regulus regulus*	Insectivore (foliage)	Green
Grasshopper Warbler	GH	*Locustella naevia*	Insectivore (low foliage)	Amber (Red in UK)
Great Tit	GT	*Parus major*	Insectivore (foliage)	Green
Grey Wagtail	GL	*Motacilla cinerea*	Insectivore (ground & aerial)	Green (Amber in UK)
Long-tailed Tit	LT	*Aegithalos caudatus*	Insectivore	Green
Meadow Pipit	MP	*Anthus pratensis*	Insectivore (ground)	Green (Amber in UK)
Mistle Thrush	M.	*Turdus viscivorus*	Insectivore (ground)	Green (Amber in UK)
Pied Wagtail	PW	*Motacilla alba*	Insectivore (ground & aerial)	Green
Ringed Plover	RP	*Charadrius hiaticula*	Insectivore	Amber
Robin	R.	*Erithacus rubecula*	Insectivore (ground)	Green
Sand Martin	SM	*Riparia riparia*	Insectivore (aerial)	Amber
Sedge Warbler	SW	*Acrocephalus schoenobaenus*	Insectivore (low foliage)	Green
Skylark	S.	*Alauda arvensis*	Insectivore (ground)	Amber (Red in UK)
Snipe	SN	*Gallinago gallinago*	Insectivore (ground)	Amber
Song Thrush	ST	*Turdus philomelos*	Insectivore (ground)	Green (Red in UK)
Spotted Flycatcher	SF	*Muscicapa striata*	Insectivore (aerial)	Amber (Red in UK)
Starling	SG	*Sturnus vulgaris*	Insectivore (ground)	Amber (Red in UK)
Stonechat	SC	*Saxicola torquatus*	Insectivore (ground)	Green
Swallow	SL	*Hirundo rustica*	Insectivore (aerial)	Amber
Wheatear	W.	*Oenanthe oenanthe*	Insectivore (ground)	Amber
Willow Warbler	WW	*Phylloscopus trochilus*	Insectivore (foliage)	Green (Amber in UK)
Wren	WR	*Troglodytes troglodytes*	Insectivore (ground)	Green
Chaffinch	CH	*Fringilla coelebs*	Granivore	Green
Goldfinch	GO	*Carduelis carduelis*	Granivore	Green
Greenfinch	GR	*Carduelis chloris*	Granivore	Green
House Sparrow	HS	*Passer domesticus*	Granivore	Amber (Red in UK)
Linnet	LI	*Carduelis cannabina*	Granivore	Amber (Red in UK)
Lesser Redpoll	LR	*Carduelis cabaret*	Granivore	Green (Red in UK)
Reed Bunting	RB	*Emberiza schoeniclus*	Granivore	Green (Amber in UK)
Wood Pigeon	WP	*Columba palumbus*	Granivore	Green
Jackdaw	JD	*Corvus monedula*	Omnivore	Green
Pheasant	PH	*Phasianus colchicus*	Omnivore	Green
Rook	RO	*Corvus frugilegus*	Omnivore	Green

Hooded Crow/Carrion Crow	HC	*Corvus cornix*	Scavenger	Green
Magpie	MG	*Pica pica*	Scavenger	Green
Raven	RN	*Corvus corax*	Scavenger	Green
Grey Heron	H.	*Ardea cinerea*	Predator	Green
Kestrel	K.	*Falco tinnunculus*	Predator	Amber
Bullfinch	BF	*Pyrrhula pyrrhula*	Frugivore	Green (Amber in UK)
Red Grouse	RG	*Lagopus lagopus scotica*	Herbivore	Red (Amber in UK)

5.4.4 Ordination analysis

NMS ordination explained 78.8% of the variation in the species density data in 2007, with Axis 1 accounting for 64.5% and Axis 2, 14.3% (**Fig. 5.3**). Axis 1 was most strongly correlated with altitude, as well as a variety of soil, habitat and plant group variables (**Table 5.2**). The majority of species were negatively correlated with altitude, with the exception of meadow pipit, skylark and wheatear (*Oenanthe oenanthe*) (see **Appendix A S5.1** - **S5.6**). Axis 2 was mainly correlated with habitat type and diversity but also with management variables such as grazing state, % dung, % vegetation litter and % signs of grazing (**Table 5.2**). Most species appeared to be negatively affected by habitat or grazing management, with the exception of wren (*Troglodytes troglodytes*), stonechat (*Saxicola torquatus*), meadow pipit (**Fig. 5.4**), raven (*Corvus corax*) and lesser redpoll (*Carduelis cabaret*). Only stonechat, raven and lesser redpoll were associated with habitat or management alone, and all positively.

NMS Ordination explained 83.4% of the variation in the species density data in 2008, with Axis 1 accounting for 71.3% and Axis 2, 12.0% (**Fig. 5.5**). Axis 1 was significantly correlated with altitude and habitat variables, while Axis 2 was not influenced by any variable measured that year (**Table 5.2**). Only two species were not affected by altitude: chough (*Pyrrhocorax pyrrhocorax*) and common sandpiper (*Actitis hypoleucos*). As in 2007, meadow pipit, skylark and wheatear were the only species to be positively associated with altitude. However, it appears that all three species are more strongly associated, albeit negatively, with Axis 2 than with Axis 1. This suggests that Axis 2 might reflect a variable inversely related to altitude.

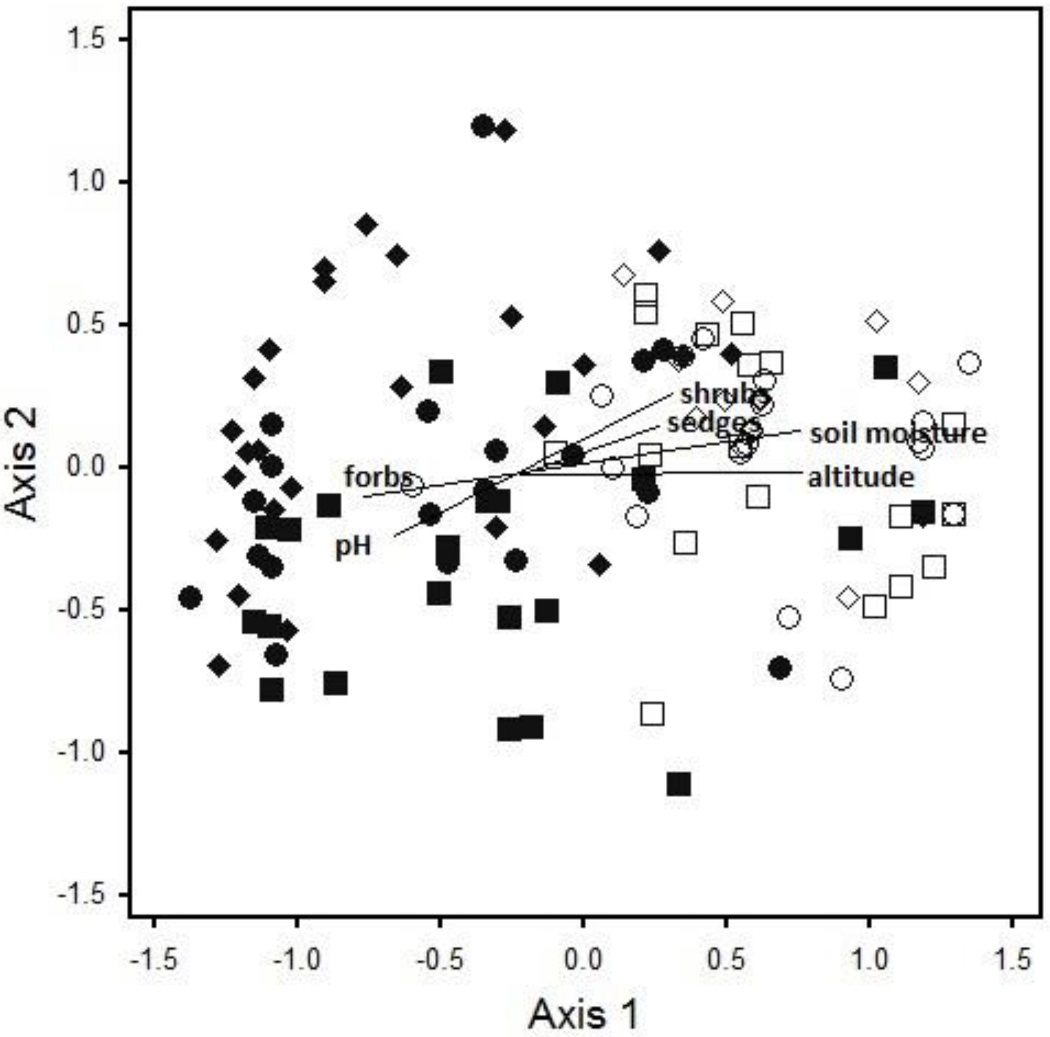

Fig. 5.3 NMS biplot of bird species densities in 2007. Closed symbols represent the lowlands (< 200m), while open symbols represent the uplands (> 200m). Diamonds represent grazing state 1 (lightly grazed), circles represent grazing state 2 (lightly-moderately grazed) and squares represent grazing state 5 (heavily grazed). Axis 1, $r^2 = 0.65$, Axis 2, $r^2 = 0.14$, cumulative $r^2 = 0.79$. Final instability = 0.00094. Stress for 2D solution = 19.608.

NMS Ordination explained 75.3% of the variation in the species density data in the lowlands in 2007, with Axis 1 accounting for 10.3%, Axis 2, 9.0% and Axis 3, 56.1%. Axis 1 was related to habitat diversity and grazing state, Axis 2, shrub cover and Axis 3, soil and plant group. There was no altitudinal gradient as the data had already been split into uplands (> 200m) and lowlands (< 200m). Wren, stonechat, lesser redpoll and blue tit (*Cyanistes caeruleus*) were negatively correlated with habitat diversity and grazing state, while swallow (*Hirundo rustica*), starling (*Sturnus vulgaris*) and pied wagtail (*Motacilla alba*) were among the species positively affected. Starling was one of the five species negatively associated with shrub cover, while willow warbler (*Phylloscopus trochilus*), wren and snipe (*Gallinago gallinago*) were among the species positively influenced. Soil and plant group had a strongly positive effect on meadow pipit, skylark and stonechat but a highly negative impact on, among others, robin (*Erithacus rubecula*), blackbird (*Turdus merula*) and swallow.

NMS Ordination explained 80.6% of the variation in the species density data in the lowlands in 2008, with Axis 1 accounting for 62.6% and Axis 2, 18.0% of the variance. Axis 1 was correlated with habitat diversity and some management variables, while Axis 2 was again, not influenced by any variable measured in 2008. Only stonechat was found to be solely influenced by Axis 2. This influence was negative, suggesting that Axis 2 may be explained by a management variable which was not measured that year. The majority of species were positively correlated with habitat diversity, with the exception of meadow pipit, skylark, wheatear and snipe.

NMS Ordination explained 72.0% of the variation in the species density data in the uplands in 2007, with Axis 1 accounting for 36.5% and Axis 2, 35.5%. Axis 1 suggested an influence of altitude, soil variables, plant groups and plant species richness, while Axis 2 was related to grazing management. Although only observations above 200m were included in this analysis, an altitudinal effect remained. Meadow pipit was most positively correlated with Axis 1 and wren most negatively. Meadow pipit was again most positively correlated with Axis 2, while skylark was most negatively affected.

Table 5.2 Ordination axes and corresponding significant correlations for variables and data sets.

Year	Data set	Habitat/environmental variable	Ordination axis	Correlation	P
2007	All	Alt:state	1	$r_s = 0.367$	$p < 0.0001$
			2	$r_s = -0.270$	$p = 0.003$
		State	1	$r_s = 0.180$	$p = 0.05$
			2	$r_s = -0.357$	$p < 0.0001$
		Altitude	1	$r_s = 0.705$	$p < 0.0001$
			2	$r_s = 0.233$	$p = 0.011$
		Habitat type	1	$r_s = 0.451$	$p < 0.0001$
			2	$r_s = 0.412$	$p < 0.0001$
		Vegetation height	1	$r_s = -0.207$	$p = 0.024$
			2	$r_s = 0.224$	$p = 0.014$
		Soil depth	1	$r_s = 0.311$	$p = 0.001$
		Soil pH	1	$r_s = -0.634$	$p < 0.0001$
			2	$r_s = -0.232$	$p = 0.011$
		Soil nitrogen	1	$r_s = 0.524$	$p < 0.0001$
			2	$r_s = 0.209$	$p = 0.023$
		Soil carbon	1	$r_s = 0.343$	$p < 0.0001$
		% soil moisture	1	$r_s = 0.593$	$p < 0.0001$
			2	$r_s = 0.277$	$p = 0.002$
		% Moss cover	1	$r_s = 0.380$	$p < 0.0001$
			2	$r_s = 0.365$	$p < 0.0001$
		% Bare ground	1	$r_s = 0.254$	$p = 0.005$
		% Dung	2	$r_s = -0.332$	$p < 0.0001$
		% Vegetation litter	2	$r_s = 0.255$	$p = 0.005$
		% Signs of grazing	2	$r_s = -0.293$	$p = 0.001$
		% Grass cover	2	$r_s = -0.239$	$p = 0.009$
		% Forb cover	1	$r_s = -0.546$	$p < 0.0001$
		% Sedge cover	1	$r_s = 0.489$	$p < 0.0001$
		% Shrub cover	1	$r_s = 0.523$	$p < 0.0001$
			2	$r_s = 0.320$	$p < 0.0001$
		% Rush cover	1	$r_s = 0.251$	$p = 0.006$
		Plant diversity	1	$r_s = -0.181$	$p = 0.049$
		Habitat diversity	2	$r_s = 0.401$	$p < 0.0001$
		Habitat richness	2	$r_s = 0.290$	$p = 0.001$
2008	All	Alt:state	1	$r_s = 0.414$	$p < 0.0001$
		State	1	$r_s = 0.278$	$p = 0.002$
		Altitude	1	$r_s = 0.666$	$p < 0.0001$
		Habitat type	1	$r_s = 0.318$	$p < 0.0001$
		% Bare ground	1	$r_s = 0.338$	$p < 0.0001$
		Habitat diversity	1	$r_s = -0.213$	$p = 0.020$
		Habitat richness	1	$r_s = -0.190$	$p = 0.039$
2007	Lowlands	Alt:state	1	$r_s = 0.376$	$p = 0.002$
		State	1	$r_s = 0.376$	$p = 0.002$
		Habitat type	3	$r_s = 0.484$	$p < 0.0001$
		Soil depth	3	$r_s = 0.269$	$p = 0.026$
		Soil pH	3	$r_s = -0.640$	$p < 0.0001$
		Soil N	2	$r_s = 0.280$	$p = 0.021$
			3	$r_s = 0.596$	$p < 0.0001$
		Soil C	3	$r_s = 0.443$	$p < 0.0001$
		% soil moisture	3	$r_s = 0.620$	$p < 0.0001$
		% moss cover	3	$r_s = 0.485$	$p < 0.0001$
		% forb cover	2	$r_s = -0.282$	$p = 0.020$
			3	$r_s = -0.580$	$p < 0.0001$
		% Sedge cover	3	$r_s = 0.487$	$p < 0.0001$
		% Shrub cover	2	$r_s = 0.354$	$p = 0.003$
			3	$r_s = 0.510$	$p < 0.0001$

		Habitat diversity	1	r_s = -0.550	p < 0.0001
		Habitat richness	1	r_s = -0.441	p < 0.0001
		Habitat evenness	3	r_s = 0.297	p = 0.014
2008	Lowlands	Habitat type	1	r_s = -0.343	p = 0.011
		% dung	1	r_s = 0.298	p = 0.029
		% vegetation litter	1	r_s = -0.292	p = 0.032
		% signs of grazing	1	r_s = 0.380	p = 0.005
		Habitat diversity	1	r_s = 0.404	p = 0.002
		Habitat richness	1	r_s = 0.367	p = 0.006
2007	Uplands	Altitude	1	r_s = 0.370	p = 0.008
		Habitat type	1	r_s = 0.280	p = 0.047
		Soil depth	1	r_s = 0.466	p = 0.001
		Soil pH	1	r_s = -0.308	p = 0.028
		% Bare ground	2	r_s = -0.330	p = 0.018
		% Dung	2	r_s = -0.281	p = 0.046
		% Forb cover	1	r_s = -0.402	p = 0.003
			2	r_s = 0.277	p = 0.049
		% Shrub cover	1	r_s = 0.292	p = 0.038
		% Rush cover	1	r_s = 0.278	p = 0.048
		Plant species richness	1	r_s = -0.405	p = 0.003
2008	Uplands	Alt:state	1	r_s = 0.367	p = 0.003
		State	1	r_s = 0.369	p = 0.002
		Habitat evenness	2	r_s = 0.259	p = 0.037

NMS Ordination explained 85.6% of the variation in the species density data in the uplands in 2008, with Axis 1 accounting for 49.1% and Axis 2, 36.5%. Axis 1 appeared to be related to grazing state and Axis 2, habitat evenness. No species were positively associated with grazing state in the uplands in 2008, although the species most negatively affected was wren. Chough and wren were among the species positively correlated with habitat evenness, while meadow pipit, skylark and wheatear were negatively influenced.

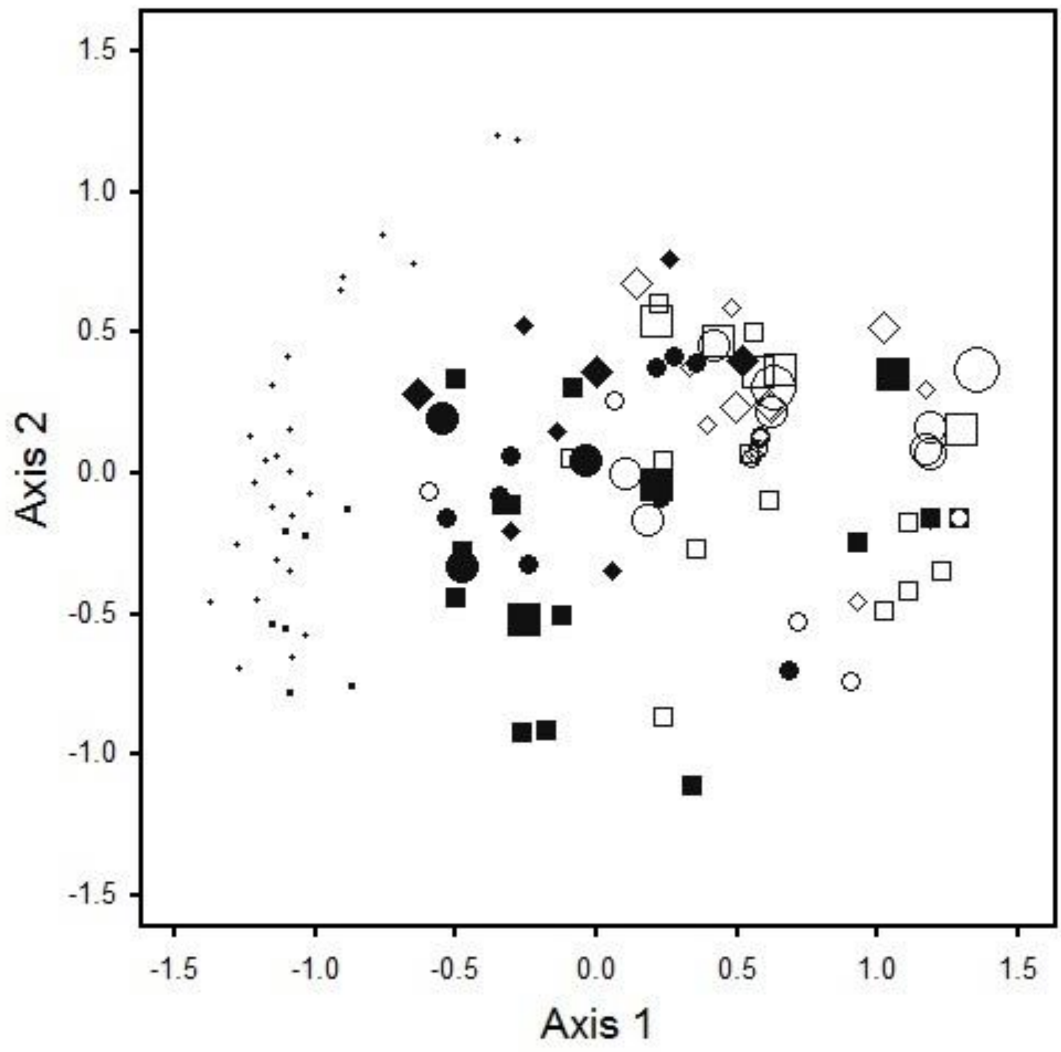

Fig. 5.4 NMS biplot of meadow pipit density in 2007. Closed symbols represent the lowlands (< 200m), while open symbols represent the uplands (> 200m). Diamonds represent grazing state 1 (lightly grazed), circles represent grazing state 2 (lightly-moderately grazed), squares represent grazing state 5 (heavily grazed). The larger the symbol, the greater the meadow pipit density. Environmental gradients are as in Fig. 5.1. Axis 1, $r^2 = 0.67$, $P < 0.0001$.

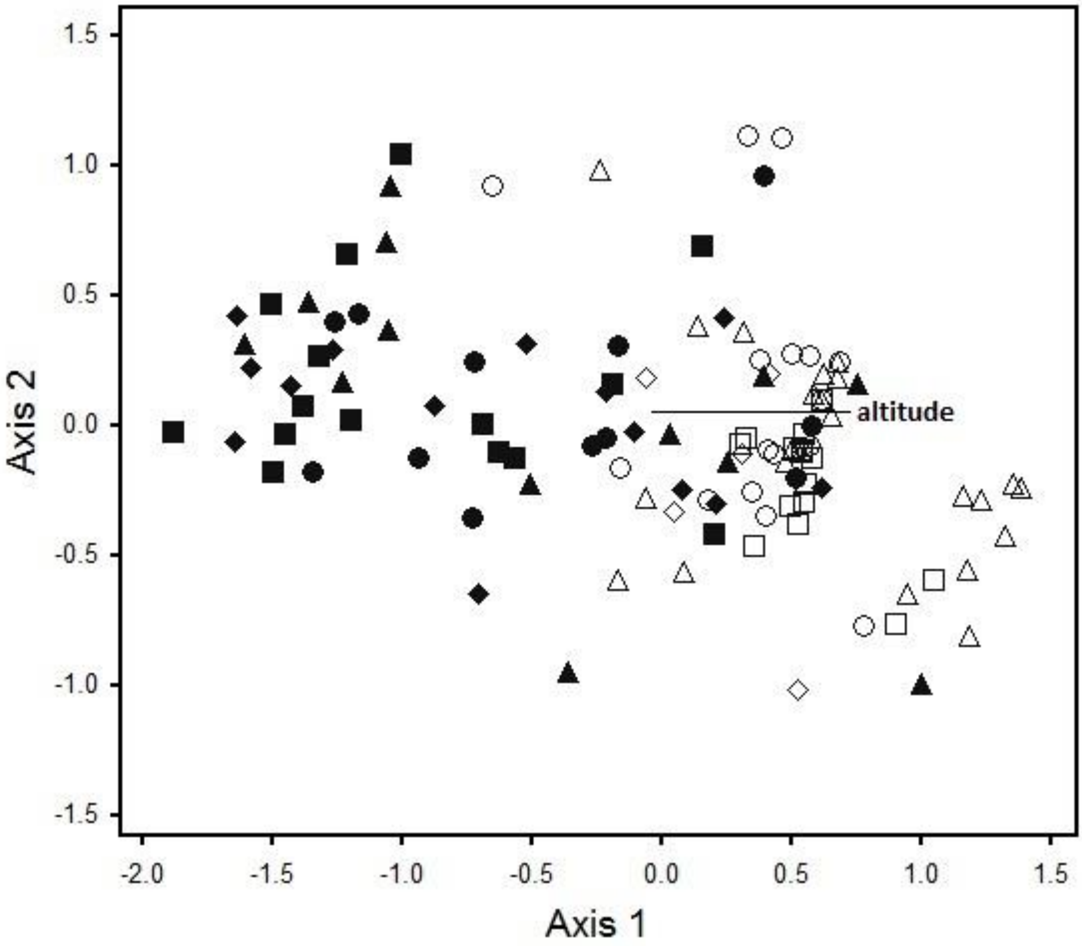

Fig. 5.5 NMS biplot of bird species densities in 2008. All closed symbols represent the lowlands (< 200m), while open symbols represent the uplands (> 200m). Diamonds represent grazing state 1 (lightly grazed), circles represent grazing state 2 (lightly-moderately grazed), squares represent grazing state 3 (moderately grazed) and triangles represent grazing state 5 (heavily grazed). Axis 1, r^2 = 0.71, Axis 2, r^2 = 0.12, cumulative r^2 = 0.83. Final instability = 0.009. Stress for 2D solution = 18.366.

5.5 Discussion

5.5.1 Grazing state and management variables

In 2007 grazing state explained around 10-14% of the variation in bird assemblage and when grazing state itself was not important, other management variables such as % bare ground, % dung, % vegetation litter, % signs of grazing or % rushes explained a large proportion of the variation in both years. Grazing state influenced upland bird assemblages to a greater degree, explaining 35-49% of the variation in both years. Godinho and Rabaca (2011) also found that grazing management is crucial in the maintenance of bird communities. Changes in bird species composition will occur over time and some of this will be the result of succession, however some will also be related to grazing management (Pollock *et al*., 2005). Some bird species require a threshold of grazing density (and a high cover of dung and bare ground) to be reached before they can breed (Kamp *et al*., 2009). Different levels of grazing may also be required at certain times of the year, for example, nest survival was greater for some ground nesting species in areas with more bare ground, while lower levels of grazing were required by chicks which were at risk from trampling by cattle (Norris *et al*., 1997; Pavel, 2004; Pollock *et al*., 2005; Watson *et al*., 2006). Chick size or egg mass may actually be a good indicator of habitat quality (Warkentin *et al*., 2004). Other studies, however, have found no effect of grazing on bird density or distribution (Medin and Clary, 1991; Goguen and Mathews, 1998; Smythe and Haukos, 2010; Hanspach *et al*., 2011).

Differences in bird diversity between sites may also be explained by variation in food supply (Söderström and Pärt, 2000). The majority of insectivores found on moderately or heavily grazed farms were ground feeders, while those on lightly grazed farms were mainly foliage invertebrate feeders. This suggests that grazing had an effect on insectivorous birds, as supported by Atkinson *et al*. (2005), who found that intensive grazing in the winter encouraged more soil invertebrate feeders, who tended to avoid tall swards in the summer. Lantschner and Rusch (2007), however, found no evidence that grazing affected insectivores. Canaday (1997) suggested that a reduction in insectivorous birds through human impact may have been the result of decreased prey levels or perhaps insectivores have greater habitat sensitivity and higher ecological specialisation. This places them at a disadvantage when in competition with opportunistic disturbance-adapted omnivores, which have been found in equal numbers on all grazing states in the present study.

Heavily grazed sites contained the greatest number of species of conservation concern. This may reflect the fact that many open habitat species are in decline, while scrub and woodland species are generally more common (Tucker and Evans, 1997; Woodhouse *et al*., 2005). In Europe 33% of grassland bird species, for example, are threatened, while only 4% of woodland species have unfavourable status (Laiolo *et al*., 2004).

The lowest number of species, over all states, was consistently found on lightly-moderately grazed farms. Perhaps the intermediate nature of this state constitutes a lack of suitable habitats for birds which favour either lightly or moderately grazed locations. It has been suggested that if a habitat declines in quality an individual may substitute the lack of preferred habitat with that of a matrix habitat, known as the 'habitat compensation hypothesis' (Norton *et al*., 2000; Brotons *et al*., 2005). They may also be able to supplement the poorer habitat with resources from neighbouring habitats, as in the 'habitat or landscape supplementation hypothesis' (Dunning *et al*., 1992; Brotons *et al*., 2005). However, often, the focal and surrounding habitats are not of sufficient quality, resulting in low species richness and abundance, as in the 'fragmentation hypothesis' (Debinski and Holt, 2000; Brotons *et al*., 2005).

A core group of species were found across all grazing states: meadow pipit, wren, chaffinch, dunnock, blackbird, robin and swallow. It does not appear that grazing state has a sizeable effect on any individual bird species, although stonechat and linnet were generally only recorded in lightly or lightly-moderately grazed states, while starling and pied wagtail were most common in heavily grazed states. Swallow, starling and pied wagtail, and to some extent skylark, were positively associated with a higher level of grazing, while wren and stonechat were not. Other studies have shown that starling and pied wagtail prefer shorter swards or bare ground (Atkinson *et al*., 2004), as does skylark (Laiolo *et al*., 2004). Raven, unexpectedly, were found to be negatively associated with grazing in the present study, unlike previous work which has shown raven density to be higher in grazed habitats (Delestrade, 2002).

One bird species noticeable by its absence in the present study is the upland breeding wader, the curlew (*Numenius arquata*), although its preferred habitats of upland peatland and unimproved grassland (Henderson *et al*., 2002) are abundant across County Kerry. However they have been shown to prefer raised bog to blanket bog (Bracken *et al*., 2008), which is less common in the study area. One explanation may be an increase in predator populations such as crows and foxes, or the fragmentation of breeding habitat, with the replacement of rough grazing with permanent grassland (Grant *et al*., 1999). However, the severe decline in breeding curlew populations in Ireland is most likely as a result of grassland intensification and the exploitation of peatland through cutting or drainage (Denniston, 2012).

The % dung, % signs of grazing, % vegetation litter and vegetation height (cm) are all direct indicators of grazing intensity, while plant groups such as shrubs or rushes can be seen as indirect indicators of grazing management, as they will take longer to alter after a change in grazing management. Although in the present study direct effects of grazing management have been shown to influence bird assemblage, previous studies have only found weak evidence of a link between direct management practices and birds, observing that indirect effects such as plant community structure or species richness were found to be of greater significance (Woodcock *et al*., 2009), although this is often dependent upon the size of the area grazed (Fontaine *et al*., 2004). Moreira *et al*. (2005) found that while farmland bird abundance was affected by management at the field scale, bird assemblage was actually influenced to the greatest extent by landscape diversity.

5.5.2 Altitude

In the present study, altitude was the most important environmental characteristic across all farms and explained almost three quarters of the variation in bird assemblage composition. This corresponds with previous studies (Brown and Stillman, 1993; Fuller *et al*., 1997). As one might expect, the lowlands were more species rich than the uplands (Rolando *et al*., 2007), and this difference may be explained by the effect of thermo-energy on body size (Lebreton and Girard, 2005). The insectivores followed the same pattern as the majority of birds, while scavengers were found in equal numbers in the uplands and lowlands. Granivores, however, were almost completely absent from the uplands. The uplands supported a consistent number of species of conservation concern across all farms, however, the lowlands were quite variable, perhaps reflecting the differing availability of open habitat. In fact open habitat bird species are generally confined to higher altitudes (Laiolo *et al*., 2004).

Axis 2 in 2008 could not be attributed to any one variable, although further investigation showed that the birds which were positively associated with Axis 1 (altitude) were negatively associated with Axis 2, suggesting an inverse relationship between these axes. This unexplained variation could be attributed to a decrease in scrub cover or vegetation height, as scrub regeneration is less likely at higher altitudes (Gillings *et al*., 2000). It may reflect a decrease in grazing intensity with elevation (Laiolo *et al*., 2004), which was not detected by measured variables, or perhaps the reduction in stone walls or hedgerows with increasing altitude. Another possibility is that the variation may be due to a variable not measured in 2008, such as a soil characteristic or plant group.

Across both years, three individual species were always found in higher densities in the uplands than in the lowlands – meadow pipit, skylark and wheatear. The positive association of meadow pipit and skylark with altitude supports the findings of previous studies (Browne and Stillman, 1993; Chamberlain and Gregory, 1999; Browne *et al*., 2000; Smith et al., 2001; Pollock *et al*., 2005; Copland *et al*., 2012). The majority of species were more abundant in the lowlands and many were rarely found above 200m. The large areas of blanket bog, moorland, and the shorter vegetation could all benefit these species. All three are ground feeding insectivores and tend to be associated with open, grazed or unimproved grassland (Henderson *et al*., 2004), suggesting that vegetation height may be important. The wheatear is a vulnerable species and meadow pipit populations in Ireland have shown a decline over the last ten years (Crowe *et al*., 2010). However, as in previous studies, the most abundant bird species of the uplands in the present study remained the meadow pipit (Ratcliffe, 1990; Fuller *et al*., 1999; Smith *et al*., 2001). The wren was the second most abundant species in the uplands and the most abundant in the lowlands. The high abundance of wren, and lower abundance of skylark, could reflect the lack of open upland habitat in the present study. Previous studies have shown that habitat accessibility is important to meadow pipit, as sites with lower vegetation height were selected to a greater extent (Douglas *et al*., 2008) as were sites with a lower proportion of the grass *Molinia caerulea* (Vandenberghe *et al*., 2009). An intermediate level of heather is important for meadow pipit (Pearce-Higgins and Grant, 2006), as are heather, bog and grassland mosaics (Vanhinsbergh and Chamberlain, 2001). Skylark, a farmland specialist and species of conservation concern (the Red UK list and the Amber Irish list), was the third most abundant species in the uplands in the present study. Some studies have shown that although arable land is of greater importance to skylark than the uplands, grasslands still support high densities (Wakeham-Dawson *et al*., 1998; Chamberlain and Gregory, 1999; Browne *et al*., 2000). In fact, pastoral farms have been found to support many more declining seed-eating bird species than arable farms, which tend to support more stable or increasing species (Siriwardena *et al*., 2000). This may be the result of pastoral farms having smaller field sizes and therefore greater hedgerow densities, as well as differing from arable farms in the timing, nature and quantity of pesticide and fertiliser inputs. However species-specific preferences for nesting sites and foraging areas will also play a role and it is the interaction between these species-specific habitat requirements and farming practices which will determine the presence of particular bird species (Siriwardena *et al*., 2000). Although crop height was found to be more important than habitat diversity to skylark (Chamberlain *et al*., 1999), a rise in habitat diversity has been shown to increase skylark density, but only in the uplands (Chamberlain and Gregory, 1999). However, in Ireland, land use differs markedly from that in Britain and skylarks are rarely found in crops, displaying a greater preference for open unimproved grasslands (Copland *et al*., 2012). Skylark are known to be associated more with grassy upland habitats than heath, and have been suggested as a good indicator species for grasslands (Baldi *et al*., 2005). They require short grass, preferably seeding (Perkins *et al*., 2000; Pearce-Higgins and Grant, 2006; Bracken *et al*., 2008). Although skylark are almost as widespread as meadow pipit, they are generally found in much lower numbers (Ratcliffe, 1990; Chamberlain and Gregory, 1999; Browne *et al*., 2000), especially in the presence of high predator density, such as kestrel (*Falco tinnunculus*) (Martinez-Padilla and Fargallo, 2008). Although skylark are within the ten most common species in the EU25 countries and the UK, and within the twenty most common species in Ireland, they are showing a moderate continued decline throughout Europe (Newton *et al*., 1999; BirdLife International, 2004; Coombes *et al*., 2006; Coombes *et al*., 2009; Eaton *et al*., 2009; PECBMS, 2009), particularly, along with wheatears, in marginal upland grasslands (Henderson *et al*., 2004). The importance of upland habitats for skylark therefore indicates the necessity for a consensus on management guidelines at both the national and international scale (Gregory and Baillie, 1998).

The majority of bird species in the present study were mainly affected by altitude, such as robin, blackbird and chaffinch (*Fringilla coelebs*), all generally lowland species. In agreement with previous work, wren, however, although more diverse in the lowlands, was not confined by altitude and its habitats ranged from the stone walls and hedgerows surrounding lowland farmsteads, to the highest mountain crags (Ratcliffe, 1990). Despite wren, robin, blackbird and chaffinch being the most widespread species in Ireland, rook (*Corvus frugilegus*) were actually the most abundant (Coombes *et al*., 2006; Coombes *et al*., 2009). This species was almost never recorded in the present study, presumably as a result of the lack of suitable habitat, such as tree stands. Wren are more common in Ireland and the UK than in the EU25 countries (BirdLife International, 2004). Wren and robin also constitute a larger percentage of farmland bird populations in Ireland than in the UK, possibly as a result of higher hedgerow density, due to smaller field sizes in Ireland (Lysaght, 1989; Siriwardena *et al*., 2000).

5.5.3 Habitat

Both habitat type and habitat diversity played a role in determining bird assemblage in both years in the present study, particularly in the lowlands. The highest number of species was recorded on improved grassland, lowland blanket bog and scrub, with improved grassland containing the greatest number of insectivores, granivores and species of conservation concern, suggesting that anthropogenically managed habitat was of importance to many bird species. One explanation may be that improved grassland is usually surrounded by stone walls, hedgerows or treelines, which are key habitat features for many bird species. Improved grassland is also generally an open habitat, which is becoming increasingly uncommon. However, Wilson *et al*. (2012) found that open habitat specialists are scarce or absent from areas of improved grassland, suggesting that in the long term, an increase in shrub and tree cover may potentially benefit the birds in these sites. However, this may depend on whether the birds were migrant or resident species (Fuller and Crick, 1992). It may be that although heavily managed, improved grassland contains a poorer diversity of invertebrates, unless soil productivity is particularly high, birds are forced to compromise and favour the easier foraging supplied by short grass and open ground (Atkinson *et al*., 2004; Woodhouse *et al*., 2005).

Interestingly in the present study, the % scrub on a farm was found to have a positive effect on bird density. Bird density increased until the % scrub per farm reached 16%, after which it began to decline again. This is with the exception of two moderately grazed farms with little scrubland which gave rise to high bird densities. Perhaps these farms contained other structural characteristics, such as a greater number of hedgerows or perhaps the moderate level of grazing was sufficient to compensate for the lack of scrub. These findings were supported by Nikolov (2010) who recommends the inclusion of approximately 15% scrubland, wherever achievable. Scrub is used by a wide range of bird species and may provide essential resources at certain times of the year. However the composition of bird communities within scrub will vary depending on the mosaic of vegetation types present, the successional stage and geographical location (Fuller *et al*., 1999; Gillings *et al*., 2000; Mortimer *et al*., 2000). Bird community composition has been shown to be closely related to scrub structure and successional stage. Wren and robin, for example, are scarce in open scrub habitat, only colonising once the canopy becomes more closed (Fuller *et al*., 1999). Upland scrub, dominated by *Ulex gallii*, has been found to support 20 - 30 bird species and is more diverse than open moorland alone (Gillings *et al*., 1998; 2000). Although some argue that bird diversity, as a measure, only reflects the heterogeneity of a habitat rather than the quality (Laiolo *et al*., 2004), which may be more dependent upon the abundance, performance or condition of birds (Johnson, 2007). It has been suggested that the provision of more scrub in the uplands may benefit birds of prey through the increase in small bird and mammal prey (Usher and Thompson, 1993). In fact the absence of treeline scrub in Britain, along with a lack of key invertebrate food resources and vegetation mosaics may help to explain the lack of functional support for a wider assemblage of alpine birds (Thompson *et al*., 2012). Species such as stonechat are substantially influenced by habitat. Scrub, in particular, has been shown to contain many of their prey types (Cummins and O'Halloran, 2002), while at least 50% shrub cover has also been found to be preferential for this species (Illera, 2001). In contrast, stonechat, employ a variety of foraging techniques, enabling them to take full advantage of a range of habitats (Revaz *et al*., 2008). A core group, consisting of meadow pipit, wren, chaffinch and dunnock were found in all habitats. This supports Gillings *et al*. (2000), who also found meadow pipit and chaffinch in all habitats sampled. However, unlike Gillings *et al*. (2000), the present study only found willow warbler in lowland and upland blanket bog habitats, perhaps reflecting the abundance of trees in these habitats. Meadow pipit will persist in scrub at low densities, however skylark will generally be confined to open habitat (Fuller *et al*., 1999). Snipe, in the present study, were only found on lowland blanket bog, which reflects the fact that snipe require wetter conditions (Henderson *et al*., 2004), and starling and pied wagtail were only recorded on improved grassland in the lowlands, perhaps indicating their need for shorter grass for foraging. Meadow pipit density in the present study increased as the area of upland blanket bog per farm increased. Is upland blanket bog a key habitat for meadow pipit, or is there something else about these particular farms which encourage this species? Habitat was also a key factor for wren over both years. As habitat diversity, plant species richness and % forbs increased, so too did wren density. Dunnock also appear to be consistently associated with vegetation structure and habitat.

Habitat type seems to be related to altitude, soil and plant groups, while habitat diversity is influenced to a greater extent by grazing management. In 2007 altitude, habitat type and % bare ground were associated with Axis 1, while habitat diversity and grazing state were associated with Axis 2. This corresponds with Moreira (1999) who also found that bare ground was important for birds. In 2008 the aforementioned variables were found on the same axis. Perhaps there was a greater association between altitude and habitat diversity in the farms surveyed in 2008. Habitat diversity and management variables such as grazing state, % dung, % signs of grazing or % vegetation litter always appear at opposite ends of the same axis. It suggests that grazing management may have a degree of influence over the diversity of habitats on a farm.

5.5.4 Soil, plant group and other characteristics

Due to their mobility birds utilise the landscape at a broader scale than, for example, invertebrates or plants. Therefore one would expect landscape scale variables such as altitude, slope, aspect or even local scale variables such as shrub cover to have a greater impact on birds than vegetation height or soil characteristics (Bossenbroek *et al*., 2005). In the present study vegetation height was not of particular importance. Although other studies have shown that vegetation structure and height were correlated with bird density and abundance, indicating that birds were responding to habitat heterogeneity (Boelscher, 1988; Moreira, 1999; Whitehead *et al*., 2005; Buchanan *et al*., 2007; Douglas *et al*., 2008). In some cases birds themselves may actually influence plant species composition in an area through the dispersal of seeds in soil clinging to their feet. Brose (2001) has suggested that this accurate form of dispersal may be a way to counteract the effects of fragmentation, with the aid of individual bird species (Miller and Cale, 2000). In other cases structure, as opposed to floristic composition, appears to be of more importance to birds (Lantschner and Rusch, 2007). Plant group/type, however did influence bird community structure in the present study. This is supported by Farina *et al*. (1997), who found that bird species richness and abundance were significantly correlated with vegetation type. The % forbs explained over fifty percent of the variation in bird assemblage in 2007, closely followed by the % shrubs, % sedges and % mosses. These particular plant groups may indicate other habitat characteristics favoured by birds. A high % forbs, for example, may signify high plant diversity, perhaps higher invertebrate diversity and therefore a greater food resource for insectivores.

Shrub density, in particular, is important for many bird species (Moreira, 1999; Osiejuk *et al*., 1999; Miller and Cale, 2000; Jeganathan *et al*., 2004; Godinho and Rabaca, 2011) and, as with scrub cover, 15 - 20% shrubland on moderately grazed land has been found to support a high number of bird species (Woodhouse *et al*., 2005; Brambilla *et al*., 2007; Tsiakiris *et al*., 2009). In the present study wren, willow warbler, stonechat and snipe were positively influenced by % shrub cover to the greatest extent. As they require good vegetation cover they were highly influenced by management and vegetation structure. Other studies have shown that snipe actually prefer a heterogeneous vegetation structure (Pearce-Higgins and Grant, 2006), while willow warbler require vegetation heights of between 3.7 and 5.3 metres (Bellamy *et al*., 2009).

Plant diversity was found to explain a small percentage of variation in upland bird assemblage. This may again be indicative of another variable such as invertebrate diversity as opposed to plant diversity *per se*. Although some studies have found that plant species richness does influence choice of foraging area by birds (Alder and Marsden, 2010), others have found that areas with high plant diversity do not necessarily also have high bird diversity (Pereira and da Fonseca, 2003).

As with plant groups, soil characteristics also explain a large percentage of variation in bird community structure. In the lowlands soil pH, soil moisture, soil nitrogen content and soil organic carbon content are important, while in the uplands soil depth is of greater significance. Perhaps this reflects the large areas of deep blanket bog, usually of between 1m and 7m in the uplands (Fossitt, 2000). Previous studies have also shown that soil moisture affects birds, with wetter areas containing lower densities but higher species richness of ground-nesting birds (Boelscher, 1988; Kim *et al*., 2008). Areas of wet ground are also more likely to increase invertebrate food resources (Buchanan *et al*., 2006).

When the altitudinal gradient is removed, habitat diversity, habitat type and grazing state (or management variables which reflect grazing state), appear of key importance in explaining bird composition in the lowlands. Soil characteristics and plant groups, however, also remain influential, suggesting that they might represent an altitudinal gradient or might merely reflect habitat type. In the uplands the influence of habitat remains fundamental, as does grazing state (or management variables reflecting grazing state). Although in 2007 plant groups, soil characteristics and altitude also remain influential. Perhaps the farms surveyed in 2007 consisted of a greater variation in upland habitats or maybe gradients were steeper and therefore differences in bird densities more pronounced.

5.5.5 Species densities

Skylark densities on the farms in the present study were between five and seven times lower than that of meadow pipit. Bracken *et al*. (2008) found this figure to be just over two, while Wilson (2002) noted that meadow pipit tend to outnumber skylark often by a factor of two or three on peatlands. However, densities of skylark in Ireland have been found to be relatively low compared with those recorded in Britain (Copland *et al*., 2012). Bracken *et al*. (2008) suggested that meadow pipit may be considered a peatland generalist in the breeding season as they were found on all surveyed sites, while skylark avoided fens. In the present study there were no fens and skylark, although observed at much lower densities, were found on almost all sites, with the exception of bracken and montane heath. Although wren did not avoid blanket bog, their densities were greatly reduced on bog in comparison with other habitats.

5.5.6 Management implications

This study emphasised the importance of open habitats for birds (Pollock *et al*., 2005), particularly for those of conservation concern. Small fragments of permanent grassland are considered vital refuges for many plant and invertebrate species (Cousins and Eriksson, 2001; Söderström *et al*., 2001; Tscharntke *et al*., 2002) and grasslands with patches of shrubs have been shown to have the highest conservation value for birds (Pons *et al*., 2003).

Upland and lowland bird species all vary in their preference for compositional and structural habitat features; therefore grazing management which promotes a heterogeneous mosaic will be more likely to support a diverse bird assemblage (Pearce-Higgins and Grant, 2006).

Some studies have shown, for example, that skylark avoid small fields enclosed by hedgerows or treelines (Tucker, 1992; Wilson *et al*., 1997; Wakeham-Dawson *et al*., 1998; Donald *et al*., 2001; Gillings and Fuller, 2001; Copland *et al*., 2012), and several bird species actually have minimum area requirements (Vickery *et al*., 1994). However, it is also well documented that many other species benefit from the presence of hedgerows or treelines (Hinsley and Bellamy, 2000; Batáry *et al*., 2010; Copland and O'Halloran, 2010). Unfortunately ecologically diverse traditional mixed farming systems, which promote a moderate level of grazing, are now rarely economically feasible. Therefore in order to help conserve as many bird species as possible agricultural policy reforms may be the best step forward (Wilson *et al*., 1997).

Some studies advise the consideration of broad environmental gradients in the construction of long term conservation strategies (Hanspach *et al*., 2011). It is recommended that the effects of grazing pressure on bird populations are monitored over time, across different seasons and at varying scales (Fuller and Gough, 1999). A moderate level of grazing along with patches of shrub or scrub may be the key to encouraging maximum diversity in the bird assemblage.

5.6 Conclusions

Recent changes in European agricultural policy may be observed through changes in grazing management. It is vital to understand the subsequent consequences of these changes on biodiversity. As many farmland and upland birds are in decline, studies such as this are of particular importance.

Grazing state and management variables accounted for around a third of the variation in bird community structure. Grazing management has been found to be crucial in maintaining bird communities (Godinho and Rabaca, 2011), and particularly insectivores (Atkinson *et al*., 2005), as found in the present study. Short swards are valuable feeding sites for species such as starling or pied wagtail and dunging provides a localised source of invertebrates (Fuller and Gough, 1999), while low levels of grazing are essential for species such as stonechat. Altitude explained the majority of variation in bird assemblage over both years and meadow pipit, skylark and wheatear were all found to be more common in the uplands, as found in previous studies (Brown and Stillman, 1993; Fuller *et al*., 1997; Chamberlain and Gregory, 1999; Smith *et al*., 2001). Within the altitudinal ranges (i.e. < 200m and > 200m), habitat type and grazing management factors became more significant. Habitat type was also important and the area of scrub present on a farm, in particular, was shown to have a positive influence on bird density. Others have shown that bird community assemblage is closely related to scrub structure (Fuller *et al*., 1999; Gillings *et al*., 2000). Habitat and vegetation structure are important, especially for ground-nesting and ground feeding species (Fuller and Gough, 1999). Plant group, for example, forbs, soil pH and moisture content were influential to a certain degree. Soil moisture may signify the presence of wet flushes, which are rich in invertebrate prey for insectivorous bird species (Buchanan *et al*., 2006).

Habitat heterogeneity is more likely to develop under moderate grazing (Fuller and Gough, 1999: Pearce-Higgins and Grant, 2006). However, a variety of grazing management regimes, from individual fields to whole landscapes, is central (Benton *et al*., 2003; Durant *et al*., 2008). Although the number of species gained from scrub development (Gillings *et al*., 2000), or woodland understory regeneration (Fuller *et al*., 1999), will outweigh the number lost from scrub-encroached moorland or grassland, it is vital that large-scale abandonment of grazing does not occur, particularly as upland grasslands are important refuges for species whose lowland grassland habitats are disappearing (Laiolo *et al*., 2004). In fact it is the birds of conservation concern which will suffer to the greatest degree from the decline in open habitats through abandonment of grazing (Tucker and Evans, 1997; Woodhouse *et al*., 2005). Therefore, if the desired outcome is to maximise bird diversity, then the production of coarse-grained mosaics, consisting of both open moorland and mature woodland, may provide the solution (Gillings *et al*., 2000).

The key to making reliable predictions on changes in grazing pressure is to understand the habitat requirements of different upland bird species (Fuller and Gough, 1999). An integrated approach to grazing management is recommended, determined by habitat type, altitude and policy. This will benefit the bird assemblages, the wider biodiversity and function of ecosystems, as well as the rural communities which farm the land (Brown and Stillman, 1993; Laiolo *et al*., 2004; Hanley *et al*., 2008).

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Chapter 6

Scale effects: the impact of grazing management and altitude on plant, ground beetle and bird assemblages at multiple spatial scales

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The Bridia Valley, Co. Kerry (Photo: Roz Anderson).

6.1 Abstract

There is growing awareness of the importance of spatial scale in the management of agricultural land for biodiversity, particularly in the uplands. Study of the management and environmental factors affecting the structure and function of plant and animal assemblages at multiple spatial scales will help determine their impact on ecosystem functioning and services. A hierarchical sampling design, based on three spatial scales across three taxa (plants, ground beetles and birds) was applied to estimate the effects of grazing state and altitude on the variation in community composition. Permutational multivariate analysis of variance (PERMANOVA) revealed that variation was generally greatest at the smallest spatial scale for all taxa, with the exception of the effect of grazing on plant assemblage, in which variance increased with scale. There was a significant grazing state x altitude interaction for all three taxa at the smallest spatial scale, but ground beetles also displayed a significant interaction at the medium scale. There were no significant grazing or altitude effects on plant assemblages at the largest scale. In contrast, there was for ground beetles and birds, although no significant interaction was found. Similarity percentages analysis (SIMPER) highlighted that the number of species contributing to total similarity was greatest for plants, then ground beetles and then birds and similarity generally decreased with grazing intensity, but increased with spatial scale, with the exception of ground beetle assemblages above 400m. Different taxa respond to agricultural practice at different spatial scales and often at multiple spatial scales, depending on their mobility and size. Grazing state and altitude are clearly critical factors in helping to predict assemblage structure. Therefore there is a need for agri-environment schemes to target multiple spatial scales to create landscape scale benefits.

6.2 Introduction

The uplands of Ireland and Britain consist of mosaics of vegetation communities which are determined by the underlying soil, rainfall and aspect, as well as anthropogenic impacts such as grazing by domestic livestock (Gordon and Dennis, 1996). Foraging decisions by livestock are made at a range of spatial scales – the feeding station, the vegetation patch and the landscape scale (Dennis, 2003). The effects of grazing on plant and animal species vary according to the scale of observation because large herbivores do not graze in a uniform manner (Clarke *et al*., 1995; Hester *et al*., 1999) and plant communities vary with landform, hydrology and climate (Rodwell, 1992), as well as in their response to grazing (Oom *et al*., 2002). The preference for a particular plant species varies with the proportion of the species in the sward (Gordon and Dennis, 1996) and intake of the less preferred component of the sward is determined by the availability of the preferred component, which varies with season (Grant *et al*., 1985; 1987). The structural heterogeneity caused by small scale selection by grazers is important for maintaining higher species diversity. Effects of grazing on plant populations tend to occur at the small scale, while the response of fauna will depend on the degree of sedentary behaviour of the species involved, with highly localised changes in vegetation composition and structure affecting relatively sedentary species (Gordon and Dennis, 1996). Domestic animals respond to their environment through the influence of both food preferences and social interactions (Gonyou, 1991). Social bonds between individuals within a group interact with forage availability to determine where and when sheep forage and hence the intensity to which they will graze upon a particular vegetation type (Grant and Maxwell, 1988).

Common Agricultural Policy (CAP) reform over the last decade has led to the decoupling of subsidy payments from production, which have had a particular impact on upland habitats, with their low intensity grazing and marginal profitability. These habitats are potentially at risk from land abandonment and the scale at which habitat data are collected may provide the key to the protection of these high nature value areas and the flora and fauna within them (Cole *et al*., 2010).

Biodiversity is strongly linked to ecosystem functioning and there is growing concern that a decline in the diversity of taxa such as plants, beetles and birds could adversely impact the functioning of agricultural ecosystems and therefore the sustainability of associated ecosystem services (Flynn *et al*. 2009; Cole *et al*., 2012). Measuring spatial variation is important in understanding the mechanisms and processes that structure species assemblages and therefore ecosystem functioning (Levin, 1992; Gongalsky and Cividanes, 2008; Gray *et al*., 2009). Enhancing habitat heterogeneity, through light or moderate grazing regimes for example, at the micro, local and landscape scales will benefit a range of farmland taxa (Wiens, 1989; Levin, 1992; Fuller and Gough, 1999; Gaston, 2000; Cole *et al*., 2012). However the issue is complicated because different taxa perceive and respond to their environment at different spatial scales (Addicott *et al*., 1987; Wiens, 1989; Wiens *et al*., 1997; Cushman and McGarigal, 2002; Olff and Ritchie, 2002; Tscharntke and Brandl, 2004;

Bossenbroek *et al*., 2005; González-Megías *et al*., 2007). Assemblages can also vary greatly at a particular scale (Barton *et al*. 2009) and individuals of the same species may respond to different features of the environment at different scales (Brown, 1984; Ricklefs, 1987). The spatial heterogeneity in species assemblages also has implications for the way in which biodiversity is studied (Whittaker *et al*., 2001) and managed (Barton *et al*., 2009).

Agriculture forms the dominant land use over much of the earth, although the majority of this is arable, with grazing lands making up around a third of total agricultural land use (Haberl *et al*., 2007). This shows the importance of identifying the appropriate scale at which to intervene (Gabriel *et al*., 2010), particularly as the global demand for food increases, placing even greater pressure on the land (Tilman *et al*., 2001). Patches, landscapes and regions are, in general, all protected for different reasons and small and large patches provide different benefits (Brotherton, 1996). There is a potential mismatch between the scale of management and population processes and as many agri-environment schemes rely on public expenditure, there is a need to ensure that this funding is targeted at appropriate scales (Gabriel *et al*., 2010).

Many studies focus on the effect of farming on biodiversity at the field or farm scale (Bengtsson *et al*., 2005; Fuller *et al*., 2005) but many organisms respond to the environment at larger spatial scales (Chamberlain *et al*., 2000; Donald *et al*., 2001; Benton *et al*., 2002). For example, many species require multiple resources over their life cycles or have large home ranges (Gabriel *et al*., 2010). Few studies have examined the interactive relationship between scale and pattern-driving processes such as grazing (Fuhlendorf and Smeins, 1999) and there have been limited attempts to isolate the unique contributions of various scales to bird-agriculture relationships (Moreira *et al*., 2005). Kleijn *et al*. (2001), for example, concluded that Dutch agri-environment schemes had little effect on bird populations assessed within a very small area, suggesting that small scale farm management would have greater influence on taxa with low mobility such as plants, while large scale management would be more important for mobile taxa such as birds (Gabriel *et al*., 2010). The size of the organism is also important, with small organisms generally responding to their environment at a small scale (Barton *et al*., 2009), for example, beetle assemblages may vary considerably over distances of less than 10m (Niemelä *et al*., 1992; Holland *et al*., 2005). At larger scales (100s to 1000s of metres), beetle species may be restricted to particular habitats due to fragmentation of the landscape (Davies and Margules, 1998; Kinnunen *et al*., 2001), or broader climatic factors (Judas *et al*., 2002).

The surrounding landscape has also been shown to influence on-farm biodiversity (Hendrickx *et al*., 2007; Billeter *et al*., 2008). It is important that the effects of farming on biodiversity from fine to coarse scales are addressed in order to understand the effectiveness of within-farm management, which may then encourage landscape scale ecosystem services and biodiversity to be maximised (Gabriel *et al*., 2010). Traditionally, mountain environments have been thought to support only 'simple' ecosystems, as a result of the marked decrease in species richness as altitude increases. However, the high degree of spatial complexity of mountain landscapes suggests that mountain ecosystems should be very complicated (Haslett, 1997).

Habitat heterogeneity at multiple spatial scales will be beneficial to biodiversity but it also has the potential to be reduced at a range of spatial scales by agricultural intensification. Enhancing heterogeneity is easier logistically and politically at smaller spatial scales, however, it may be more beneficial to assess the response of organisms to heterogeneity at a large spatial scale (Benton *et al*., 2003). However, wholly regional approaches may sacrifice detailed information at particular sites (Bossenbroek *et al*., 2005). Although spatial effects can often only be detected at specific scales, depending on the dispersal rates of studied organisms and their foraging radius (Aviron *et al*., 2005; Cozzi *et al*., 2008), the ability of researchers to explain patterns in community structure may also be limited by assuming that small organisms, such as beetles, respond only to environmental variables measured at fine scales or that larger and more mobile species, such as birds, respond only to broad-scale variables (Bossenbroek *et al*., 2005).

The chosen taxa are important components of farmland biodiversity in their own right, however they may also play a potential role in the provision of ecosystem services. In agricultural landscapes plant functional traits can affect the ecosystem processes of primary productivity, standing biomass, and litter decomposition, which can directly influence ecosystem services (Díaz *et al*. 2007; Lavorel *et al*. 2011; Ford *et al*., 2012; Lienin and Kleyer, 2012). The degree to which ground beetles support ecosystem services in agricultural grazing land is difficult to quantify fully (O'Neal *et al*., 2005), however, they may be of benefit as pest control agents (Lövei and Sunderland, 1996; Mair and Port, 2001; Peterson *et* *al*., 2004) or as food for farmland birds (Poulsen *et al*., 1998). Although the economic value of birds to humans has yet to be quantified, birds do provide a cultural service through bird watching, which generates valuable revenue (Whelan *et al*., 2008). The characteristics of most birds make them quite special from the perspective of ecosystem services. Through flight they can link ecosystem processes separated by great distances (Whelan *et al*., 2008). They may act as predators of arthropod pest and weed species, or as scavengers, seed dispersers or ecosystem engineers (Sekercioglu, 2006; Kellermann *et al*., 2008). However, the spatial scale over which any potential ecosystem service is generated is a vital consideration (Chee, 2004).

Here we investigate the importance of spatial scale for plant, ground beetle and bird assemblages on hill sheep farms and the potential impacts of grazing management on these taxa at varying altitudes. In particular three questions are addressed: (i) How do plant, carabid and bird assemblages vary across lightly, moderately and heavily grazed farms at different spatial scales? (ii) In what way do these assemblages change with altitudinal category? And (iii) Which species are most important in determining similarity within and dissimilarity between grazing states and altitudes?

6.3 Methodology

6.3.1 Study area

This study was undertaken on the Iveragh Peninsula (51° 94´ N, 9° 89´ W) in County Kerry, southwest Ireland. The majority of the peninsula's 1400km^2 consists of upland marginal land (O'Rourke and Kramm, 2009), often suitable only for sheep farming. Seven geographically distinct study areas were selected as being representative of upland grazing conditions on the peninsula as a whole. Within each of these areas, three hill farms subject to grazing regimes of varying intensity were chosen. The farms generally reached altitudes of 400m to 800m, although total farm areas were normally less than 250ha. Sheep stocking rates ranged from 0.06 – 0.76 LU/ha over the whole farm and 0.005 – 0.48 LU/ha in the uplands.

6.3.2 Sampling

Following an initial visit, all farm habitats were mapped (Fossitt, 2000; Hill *et al*., 2005). In total, 144 2m x 2m relevés were sampled across twelve farms on the largest four habitats of each farm. The impacts of grazing, browsing and trampling by large herbivores in upland habitats were quantified by adopting the standard methodology of MacDonald *et al*. (1998). This then allowed for the allocation of a grazing state classification (light, moderate or heavy) to each habitat and consequently each farm as a whole. To account for any spatial heterogeneity, the three class grazing state classification was smoothed into a more continuous five point classification by introducing intermediate classes light-moderate and moderate-heavy (Agresti, 1984; Brewer *et al*., 2004; Albon *et al*., 2007). The Braun-Blanquet scale was used to estimate the percentage cover of plant species: r: extremely rare, +: cover < 1%, 1: cover 1% - 5%, 2: cover 6% - 25%, 3: 26% - 50%, 4: 51% - 75%, 5: 76% - 100% (Magurran, 1988; Kent and Coker, 1992; Lepš and Hadincová, 1992).

Ground beetles were sampled over two sampling periods of three weeks duration (Dennis *et al*., 1997). Pitfall trapping was adopted, as the most widely used method for sampling ground-dwelling invertebrate assemblages (Spence and Niemelä, 1994). Six traps (plastic cups of 6.5cm diameter and 8cm depth) were placed 10m apart along the botanical sampling lines of the four largest habitats in each farm. A 1:3 mixture of ethylene glycol and water was added to the cup, as a preservative, and a few drops of detergent added to the mixture to break the surface tension (Schmidt *et al*., 2006). Covers were made from 10cm x 10cm corrugated plastic, supported about 2cm above the cup using 10cm nails. Samples were sieved, stored in ethanol and later identified to species level using taxonomic keys (Forsythe, 2000; Luff, 2007).

Birds were surveyed on each farm at the beginning of the breeding seasons of 2007 and 2008 and again at the end. They were recorded visually and by their song or call along two 1km transects, one below 200m in altitude and one above 200m, situated about 500m apart and within distance categories (within 25m, between 25 and 100m and between 100 and 300m) perpendicular to the central transect line (Bibby *et al*., 1992; Vanhinsbergh and Chamberlain, 2001; Coombes *et al*., 2006; Newson *et al*., 2009; Crowe *et al*., 2010). Counts began an hour after sunrise to avoid the dawn peak in bird activity but were not undertaken in conditions of rain or strong winds (Herzon and O'Hara, 2007). For each transect the maximum count of individuals per species from the two visits was used (Brown and Stillman, 1993; Browne *et al*., 2000; Pearce-Higgins and Grant, 2006; Herzon and O'Hara, 2007). Distance sampling software (Buckland *et al*., 1993; DISTANCE Version 5) was used to estimate bird densities (number of individuals per hectare).

6.3.3 Data analysis

To assess the influence of grazing management and altitude on multivariate patterns in plant, ground beetle and bird community structure, Bray-Curtis similarity matrixes were constructed (Bray and Curtis, 1957), which were calculated using pooled percentage cover, abundance and density data, respectively. All taxa data were analysed at three spatial scales. Plant percentage cover data: small scale: quadrats (144); medium scale: habitats (48 quadrats pooled); and large scale: farms (12 quadrats pooled). Ground beetle abundance data: small scale: pitfall traps (576), medium scale: habitats (96 traps pooled) and large scale: farms (24 traps pooled). Bird density data: small scale: 200m transects (120), medium scale: habitats which transects fell across (42 transect sections pooled) and large scale: farms (10 transects pooled). Plant percentage cover data was arcsine square root transformed into degrees to normalise possible binomial distributions (Zar, 1999; Webster and Halpern, 2010; Dorman *et al*., 2012), while ground beetle abundances and bird densities were log (x + 1) transformed, which down-weights the influence of more abundant species, whilst still allowing less abundant species to influence assemblage structure (Clarke and Warwick, 2001). Percentage cover, abundance and density measures were used rather than species richness or diversity indices, which are thought to be inadequate in characterising ecological communities on mountains (Haslett, 1997).

Community assemblages were visualised using two-dimensional non-metric multidimensional scaling (nMDS) plots, with similar samples appearing closer together and dissimilar samples plotted further apart (Clarke and Warwick, 2001). nMDS was chosen as it provides robust ordinations, resistant to quantitative noise (Minchin, 1987; Enright *et al*., 2005) and is suited to non-normal data (Clarke, 1993; McCune and Grace, 2002).

To determine whether plant, carabid or bird assemblages differed between grazing states or altitudinal ranges, permutational multivariate analysis of variance (PERMANOVA+) was applied, on the basis of Bray-Curtis similarities between samples (Anderson, 2001; 2005; Anderson *et al*., 2008; Barton *et al*., 2009; Smale *et al*., 2011). PERMANOVA is a non-parametric multivariate analogue to ANOVA that uses direct additive partitioning of variance and derives P-values using permutations (Anderson, 2001). As the Bray-Curtis similarity measure was undefined when there were two empty samples, the zero-adjusted Bray-Curtis was used, which adds a 'dummy species' to the original matrix in order to generate meaningful nMDS displays (Clarke *et al*., 2006; Bacher *et al*., 2012). Grazing state (light, light-moderate and heavy categories for plant and ground beetle analysis and light, light-moderate, moderate and heavy categories for bird analysis) and altitude (< 100m, 100-200m, 200-300m, 300-400m and > 500m categories) were treated as fixed factors. Area was treated as a random factor for all plant analysis, while month, area, farm and habitat were treated as random factors for the trap scale beetle analysis (habitat nested within farm nested within area nested with month). Month, area and farm were random factors in the beetle analysis at the habitat scale and month was treated as a random factor at the farm scale. For the birds, year, area and farm were treated as random factors (farm nested within area nested within year) at the transect and habitat scale and area and year at the farm scale (Aragón *et al*., 2010). The components of variation were extracted from the mean square (MS) estimates for each spatial scale independently, correcting for any negative estimates of variance (Fletcher and Underwood, 2002; Anderson *et al*., 2005; Chapman and Underwood, 2008). Variance partitioning can be a powerful tool in accounting for hierarchical structure (Cushman and McGarigal, 2002). Statistical significance was tested using 9999 permutations of residuals under a reduced model and Type III (partial) sums of squares, using an a priori chosen significance level of $\alpha=0.05$ (Anderson *et al*. 2008; Bacher *et al*., 2012; Giordani *et al*., 2013). Estimates of the components of variation at each scale directly translates to the estimation of spatial variation at each spatial scale (Fletcher and Underwood, 2002).

Significant terms were further examined by applying appropriate post hoc pair-wise comparisons. The Bonferroni correction was adopted as a means of adjusting significance levels to account for Type I error rates when multiple tests are applied. Each comparison was tested at 0.05/n: where 0.05 was the chosen level of significance and n was the number of comparisons or tests (Quinn and Keough, 2002).

Similarity of Percentages (SIMPER) was used in the identification of individual species which contributed the most to dissimilarities between assemblages (Davidson *et al*., 2004, Gray *et al*., 2009; Gibb and Cunningham, 2010). SIMPER analyses based on Bray-Curtis similarities, allowed for the identification of plant, ground beetle and bird species which contributed greatest to the average within group similarity and between group dissimilarity (Davidson *et al*., 2004). All analyses were performed using PRIMER (version 6.1.13, PRIMER-E Ltd., Plymouth, U.K.; Clarke & Gorley, 2006).

6.4 Results

During this study, 98 plant species, 42 ground beetle species (3927 individuals) and 56 bird species were recorded.

6.4.1 Scales of spatial variation

Variation in assemblages differed between factors and taxa. However, in general, it was greatest at the smallest spatial scale (**Fig. 6.1**). For example, the residual variability for plants at the quadrat scale, in terms of average Bray-Curtis dissimilarity among replicates, was around 27% (**Fig. 6.1**). In terms of the effects of grazing on assemblages, it appeared that variation increased with scale for plants, but decreased for ground beetles and birds. This relationship is significant at the quadrat and habitat scale for plants, the trap, habitat and farm scale for ground beetles and the transect and farm scale for birds (see following section '*Differences in assemblages*' for PERMANOVA +[1] results). These assemblages also showed a significant relationship with altitude, again at the quadrat and habitat scale for plants, at the trap, habitat and farm scale for ground beetles and at the transect, habitat and farm scale for birds. This time there was a decrease in variation with altitude, as spatial scale increased for plants and ground beetles but for birds the variation at the habitat scale was greatest. In terms of an interaction between grazing state and altitude, this too appeared to be influenced by scale. The two way interaction implies that the effect of grazing state on plant biodiversity varies with altitude, but at larger spatial scales these effects disappear and the effects of grazing state are consistent at higher altitudes. Although bird assemblages were significantly affected by the main effects of grazing state and altitude at the farm scale, a significant interaction was only found at the smallest spatial scale described by transect, which indicates that at small spatial scales the effect of grazing state on bird assemblage composition changes with altitude, but at larger spatial scales the effects of grazing state on assemblage composition are consistent as altitude increases. The effects of grazing on assemblages exhibited the greatest variation at the trap scale for ground beetles, while the effects of altitude showed the greatest variation at the habitat scale for birds. The scale of habitat presented the greatest residual variation across all taxa.

6.4.2 Differences in assemblages

6.4.2.1 Plants

Multivariate analysis (PERMANOVA +[1]) revealed that plant community assemblage varied significantly with grazing state (pseudo-F=4.7967, df=2, P(perm)=0.0001), altitude (pseudo-F=5.3824, df=4, P(perm)=0.0001) and with a grazing state x altitude interaction (pseudo-F=3.0403, df=7, P(perm)=0.0001) at the *quadrat* (small) scale. There was also a grazing state (pseudo-F=2.1033, df=2, P(perm)=0.0097) and altitude (pseudo-F=1.7794, df=4, P(perm)=0.0098) effect on plant species composition at the *habitat* (medium) scale. However, there was no significant effect on plant community assemblage at the *farm* (large) scale.

6.4.2.2 Ground beetles

Multivariate analysis (PERMANOVA +[1]) showed that ground beetle community assemblage varied significantly with grazing state (pseudo-F=2.9591, df=1, P(perm)=0.0078), altitude (pseudo-F=2.2878, df=3, P(perm)=0.0015) and with a grazing state x altitude interaction (pseudo-F=1.9586, df=6, P(perm)=0.0004) at the *trap* (small) scale. At the *habitat* (medium) scale, there was a significant grazing state (pseudo-F=2.6014, df=1, P(perm)=0.0138), altitude (pseudo-F=2.3167, df=4, P(perm)=0.0006) and a grazing state x altitude interaction (pseudo-F=1.4442, df=7, P(perm)=0.0312) effect on carabid species composition. Grazing state (pseudo-F=2.7598, df=2, P(perm)=0.0013) and altitude (pseudo-F=1.8239, df=2, P(perm)=0.0382) also played a significant role at the *farm* (large) scale, although there was no significant interaction.

6.4.2.3 Birds

Multivariate analysis (PERMANOVA +[1]) revealed that bird community assemblage varied significantly with grazing state (pseudo-F=3.0299, df=2, P(perm)=0.0003), altitude (pseudo-F=16.828, df=4, P(perm)=0.0001) and with a grazing state x altitude interaction (pseudo-F=2.0783, df=10, P(perm)=0.0002) at the *transect* (small) scale. There was also an altitude effect (pseudo-F=7.9423, df=4, P(perm)=0.0001) on bird species composition at the *habitat* (medium) scale and a grazing state (pseudo-F=1.597, df=3, P(perm)=0.0342) and altitude (pseudo-F=2.013, df=2, P(perm)=0.0129) effect at the *farm* (large) scale but again no significant interaction.

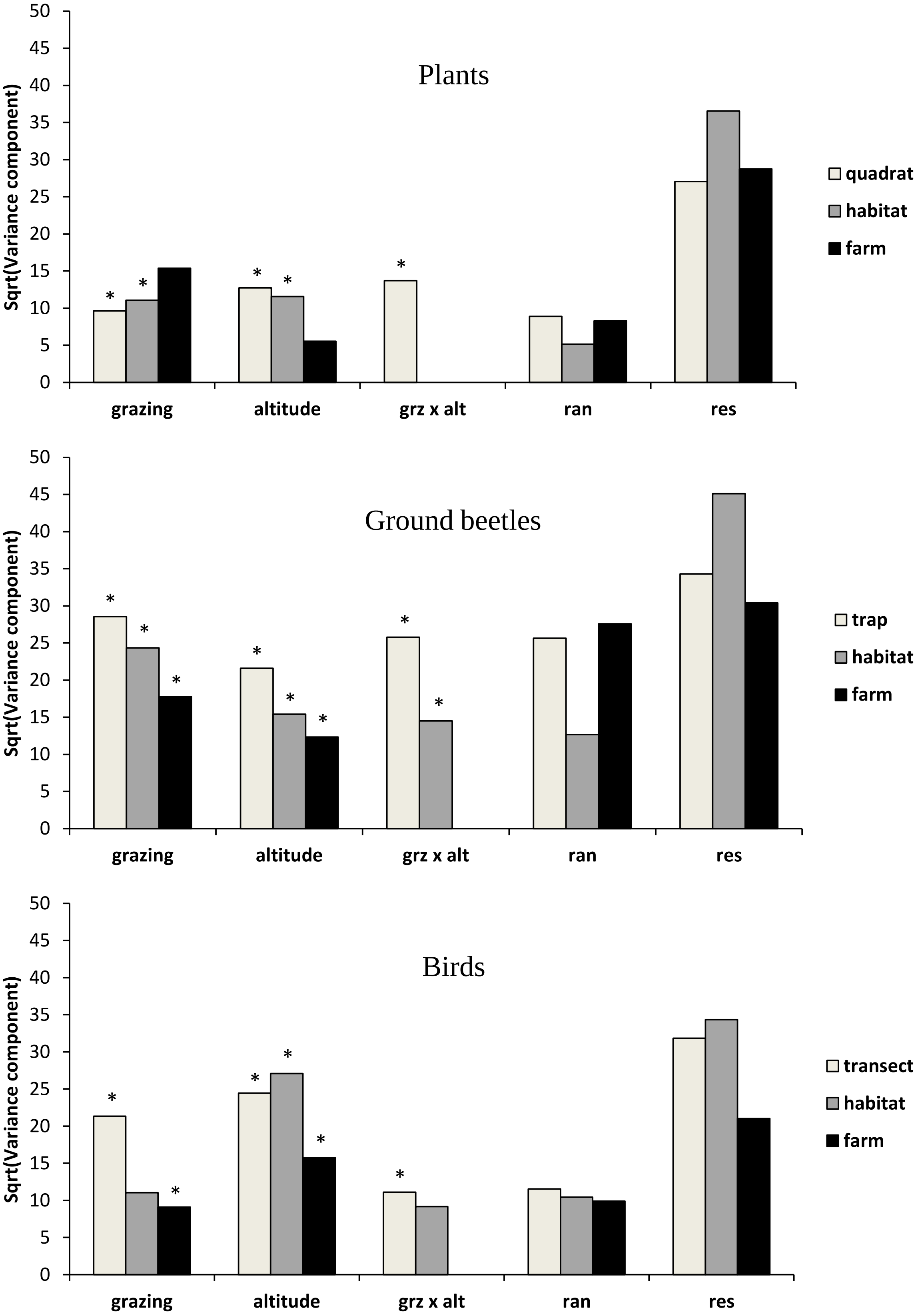

Fig. 6.1 Multivariate variance components at each of three spatial scales for plants, ground beetles and birds. The values plotted are the square root of the sizes of the variance components, obtained using mean squares from PERMANOVA. The variance attributed to random factors (eg month or year) = ran and the residual variance (variation within smallest sampling unit) = res. Missing bars indicate negative components of variation (which were set to zero and the other components then recalculated). Asterisks identify significant factors.

Post-hoc pair-wise comparisons across the grazing state x altitude interaction (PERMANOVA +[2]), highlighted significant differences in plant, ground beetle and bird community composition between grazing states within altitude categories (**Table 6.1**). These results indicated that the difference between grazing states appeared to be more pronounced between 200 and 400m for plants, which were only influenced significantly at the small scale of quadrat. At these altitudes there were significant differences between the plant assemblages of all grazing states. There were fewer significant differences between grazing states across altitudes for ground beetles, with only one significant difference (between the ground beetle assemblages of lightly and heavily grazed sites) at the trap scale and two at the habitat scale. There were significant differences between the bird assemblages of lightly and lightly-moderately grazed states between 100 and 300m at the transect scale. Although there was no significant grazing state x altitude interaction at the habitat scale, there were significant differences between the bird assemblages across altitudinal categories.

6.4.3 Assemblage structure and important species

SIMPER analysis was undertaken to determine which species contributed most towards similarity within and dissimilarity between grazing states and altitudes.

6.4.3.1 Plants

Results showed that the average percentage similarity of samples within each grazing state was 26.26%, 35.54% and 30.39% for lightly, lightly-moderately and heavily grazed, respectively. The average percentage similarity of samples within each altitudinal category was 28.33%, 23.72%, 39.85%, 38.36% and 36.96% for < 100m, 100-200m, 200-300m, 300-400m and > 400m, respectively.

Table 6.1 Significant results of PERMANOVA +^{2}, pair-wise comparisons of grazing state x altitude and altitude only across all taxa and scales. P (perm) values show the significant difference between multiple pair-wise comparisons.

taxa	scale	altitudes	grazing states	t	P(perm)	Bonferroni corrected sig.
plants	quadrat	< 100m	H, L-M	1.9215	0.0053	0.017
		100-200m	H, L	2.112	0.0004	0.05
		200-300m	H, L	2.4399	0.0002	0.017
			H, L-M	2.362	0.001	0.017
			L, L-M	1.9601	0.0038	0.017
		300-400m	H, L	2.7956	0.0045	0.017
			H, L-M	2.2147	0.0006	0.017
			L, L-M	2.1273	0.002	0.017
		> 400m	H, L-M	2.0304	0.0028	0.017
ground beetles	pitfall trap	100-200m	H, L	2.1856	0.0003	0.05
	habitat	100-200m	H, L	1.3961	0.0479	0.05
		> 400m	H, L-M	1.908	0.0047	0.017
birds	transect	100-200m	L, M	1.9431	0.0026	0.008
		200-300m	L, M	2.1115	0.0002	0.008
	habitat	100-200m, 200-300m		3.7134	0.0001	0.005
		200-300m, < 100m		2.397	0.0002	0.005
		300-400m, < 100m		2.4065	0.004	0.005
		< 100m, > 400m		2.2689	0.0014	0.005

The four most important species contributing to grazing state similarity, as well as the percentage dissimilarity between each grazing state, are listed in **S6.1** (**Appendix A**). They contributed to 58.38% of lightly grazed state similarity, 50.75% of lightly-moderately grazed and 35.05% of heavily grazed similarity. Lightly and lightly-moderately grazed states shared three of the four most important species (*Molinia caerulea*, *Potentilla erecta* and *Calluna vulgaris*), while heavily grazed states only shared one (*Potentilla erecta*). The four most prominent species contributing to altitude similarity, as well as the percentage dissimilarity between each altitude category, are listed in **S6.2**. They were found to equally influence altitudinal categories by around 50%. 51.47% similarity was attributed to the four most important species under 100m, 51.29% at 100-200m, 47.41% at 200-300m, 56.32% at 300-400m and 52.87% above 400m. *Agrostis stolonifera* and *Holcus lanatus* were only important under 100m, while *Nardus stricta* and *Erica tetralix* were only influential between 300 and 400m and *Vaccinium myrtillus* and *Juncus squarrosus* were only important above 400m.

Potentilla erecta and *Calluna vulgaris* were common to all altitudinal categories with the exception of below 100m.

The dissimilarity between grazing states appeared to be driven by the higher average percentage cover of *Molinia caerulea* (in lightly grazed sites) and *Nardus stricta* (in heavily grazed sites). The higher average percentage cover of *Holcus lanatus* and *Agrostis stolonifera* under 100m and the dominance of *Nardus stricta* between 300-400m and *Calluna vulgaris* over 400m played a part in driving altitudinal dissimilarity.

6.4.3.2 Ground beetles

Results showed that the average percentage similarity of samples within each grazing state was 12.55% (27.86% at habitat scale), 13.94% (31.19% at habitat scale) and 12.30% (22.27% at habitat scale) for lightly, lightly-moderately and heavily grazed, respectively. The average percentage similarity of samples within each altitudinal category was 17.63% (32.91% at habitat scale), 11.48% (26.05% at habitat scale), 12.47% (22.15% at habitat scale), 11.33% (24.95% at habitat scale) and 15.59% (37.58% at habitat scale) for < 100m, 100-200m, 200-300m, 300-400m and > 400m, respectively.

The four most abundant species contributing to grazing state similarity, as well as the percentage dissimilarity between each grazing state, are listed in **S6.3**. They contributed to 87.67% (74.40% at habitat scale) of lightly grazed state similarity, 64.85% (56.17% at habitat scale) of lightly-moderately grazed and 51.21% (47.66% at habitat scale) of heavily grazed similarity. *Pterostichus madidus* appeared to only be important in lightly grazed states, while *Nebria brevicollis* and *N. salina* were only important in heavily grazed states. Some carabids were only influential at the habitat scale, for example, *Carabus granulatus*, under a light level of grazing and *Pterostichus diligens* under a heavy grazing regime. The four most abundant species contributing to altitude similarity, as well as the percentage dissimilarity between each altitude category, are listed in **S6.4**. These species contributed to 66.92% (55.42% at habitat scale) under 100m, 69.53% (65.23% at habitat scale) at 100-200m, 68.57% (64.30% at habitat scale) at 200-300m, 70.89% (60.62% at habitat scale) at 300-400m and 66.55% (77.05% at habitat scale) above 400m. *Abax parallelepipidus* was the only species which appeared to be important at all altitudes. *Pterostichus niger* was not prominent above 400m, while *Carabus problematicus* was not influential below 100m. *Pterostichus madidus* was only important below 100m, while *Trechus obtusus* was only crucial above 400m and *Pterostichus rhaeticus* between 300 and 400m and above 400m. Again *Pterostichus diligens* only appeared to be influential at the habitat scale (at 200-300m), as was *P. vernalis* (below 100m).

The average ground beetle similarity at the habitat scale was twice that at the trap scale across grazing state and altitudinal categories, while the average dissimilarity and the percentage similarity or dissimilarity attributable to the four most important species was always lower at the habitat scale. This suggested that similarity between ground beetle species compositions increased as scale increased. However, there was one exception, above 400m, the percentage similarity attributable to the four most important species was lower at the trap scale, suggesting that at this elevation perhaps the carabids operate at greater spatial scales.

The dissimilarity between grazing states appeared to be driven by the higher average abundance of *Carabus problematicus* (in lightly-moderately grazed sites) and *Nebria salina* (in heavily grazed sites). The higher average abundance of *Nebria brevicollis* under 100m and the dominance of *Pterostichus niger* below 300m and *N. salina* above 200m, as well as *Carabus problematicus* above 300m, appeared to drive altitudinal dissimilarity.

6.4.3.3 Birds

Results showed that the average percentage similarity of samples within each grazing state was 41.60%, 49.36%, 52.17% and 43.36% for lightly, lightly-moderately, moderately and heavily grazed, respectively. The average percentage similarity of samples within each altitudinal category was 45.25%, 37.71%, 50.60%, 57.15% and 72.12% for < 100m, 100-200m, 200-300m, 300-400m and > 400m, respectively.

The four most important species contributing to grazing state similarity, as well as the percentage dissimilarity between each grazing state, are listed in **S6.5**. These species contributed to 71.44% of lightly grazed state similarity, 82.10% of lightly-moderately grazed, 56.06% of moderately grazed and 73.19% of heavily grazed similarity. Wren and meadow pipit appeared to influence the composition of assemblages at all levels of grazing intensity. Chaffinch and dunnock were only important under light levels of grazing, while skylark was only important under heavy grazing management. The four most prominent species contributing to altitude similarity, as well as the percentage dissimilarity between each altitude category, are listed in **S6.6**. These species contributed to 53.13% similarity under 100m, 58.51% at 100-200m, 90.04% at 200-300m, 95.06% at 300-400m and 90.79% above 400m. Wren was the only species to influence composition similarity at all altitudinal categories. Blackbird was only important below 100m, while chaffinch and robin were important below 200m. Skylark only appear to be influential between 200 and 400m in elevation. It is interesting that above 200m only three species contributed over 90% of the compositional similarity (meadow pipit, wren and skylark) and above 400m, only two species (meadow pipit and wren). However, it was meadow pipit which contributed by far the largest percentage (between 53 and 71%).

The dissimilarity between grazing states appeared to be driven by the higher average density of dunnock in lightly grazed sites, wheatear in moderately grazed sites and a higher average density of wren under all levels of grazing, with the exception of heavily grazed. Meadow pipit density was greater under all levels of grazing except lightly grazed. The higher average abundance of blackbird and swallow under 100m, robin between 100 and 200m and the dominance of wren below 400m and meadow pipit above 100m, appeared to drive altitudinal dissimilarity.

6.5 Discussion

Quantifying spatial variation in plant and animal populations is fundamental in the understanding of how ecological processes influence them. Local species abundances will change at a hierarchy of scales depending on factors such as their size, mobility or life histories (Chapman and Underwood, 2008). There are no intrinsically correct scales at which species should be measured (Levin, 1992), however it is known that small species, with rapid rates of reproduction typically show considerable small scale variability (Chapman and Underwood, 2008).

As in the present study, recent research has consistently identified organisms at small spatial scales as presenting the largest source of variability (Anderson *et al*., 2005; Gray *et al*., 2009; Barnes and Barnes, 2011; Smale *et al*., 2011), although some have found that, as with the grazing state factor for plants in the present study, the largest spatial scale exhibits the greatest variability (Tataranni *et al*., 2009). Some suggest that large scale processes are more important in determining distributions and abundances and small scale variability merely represents ‘noise’ (Hay, 1994). Others have found that large scale factors actually interact with small scale variables to determine species abundance (Gabriel *et al*., 2010).

Choosing a relevant scale for observing the mechanisms which determine patterns and processes in vegetation is crucial, be it at the small scale mosaic of individual plants or at the landscape-scale mosaic of different plant communities (Legg, 1995). Here, multivariate variation was greatest at the smallest spatial scale for plant assemblages in terms of altitude but lowest at the smallest spatial scale in terms of grazing, highlighting the significance of spatial scale on the factor under investigation. Pair-wise tests also revealed that significant differences between grazing states, within each altitudinal category, were more pronounced for plants than either ground beetles or birds, at the small scale. Plants may be more strongly affected by local management than by landscape (Stoner and Joern, 2004; Gabriel *et al*. 2006). Olff and Ritchie (1998) predicted that grazing would enhance plant species richness at small scales (due to reduced competition) and deplete richness at larger scales (due to a selection of grazing tolerant species within the species pool). However, plant species density has been found to be influenced by landscape scale effects, perhaps due to high landscape complexity, as well as local scale effects (Roschewitz *et al*., 2005; Gabriel *et al*., 2010; Rundlöf *et al*., 2010). This was not found in the present study, (although percentage cover as opposed to density was studied) perhaps because the largest spatial scale analysed was at the farm level. Perhaps the collection of data from a further set of farms to allow analysis at the landscape scale would reveal a similar story. Grazing is a key process in determining plant diversity patterns, particularly at the local scale (Oba *et al*., 2003), as found in the present study, where productivity and disturbance, along with abiotic factors such as soil pH and temperature help to structure plant diversity. At the regional scale, heterogeneity and fragmentation and the interaction between abiotic and biotic factors appear to be more relevant (Fuhlendorf and Smeins, 1999; Austrheim and Eriksson, 2001; Kohyani *et al*., 2008). By managing the distribution of grazing in relation to vegetation patterns, spatial heterogeneity can be maintained at appropriate scales, influencing ecosystem processes and biodiversity (Adler *et al*., 2001). Climatic conditions can also affect the scale at which grazing influences plants (de Bello *et al*., 2007). Plant functional groups have also been found to differ with scale (Brudvig, 2008), as have communities of rare and common plant species (Gabriel *et al*., 2006). Habitat heterogeneity across a range of scales is particularly important in the maintenance of biodiversity when habitat fragmentation becomes a problem – a phenomenon that is prevalent in mountain regions (Poore, 1992; Haslett, 1997), or when climate change influences the migration of plant species upwards on mountain peaks (Pauli *et al*., 2003).

Variation in ground beetle assemblages was greatest at the smallest spatial scale in terms of grazing, altitude and the grazing x altitude interaction and only ground beetles displayed a significant grazing x altitude interaction at more than one spatial scale. Aviron *et al*. (2005) predicted that immobile species perceive their landscape at finer scales than mobile species and are therefore influenced by their habitat at smaller spatial scales. Weibull and Östman (2003) found that landscape features explained more variation in butterfly assemblages than carabid assemblages, although Yaacobi *et al*. (2007) observed that the landscape variables were more important for carabids. Cole *et al*. (2010) found that the optimum spatial scale to collect fine-scale habitat information for immobile invertebrates was smaller than for mobile arthropods and carabids. Invertebrates may also be influenced by factors at different spatial scales due to larvae perhaps having different requirements to adults (Gabriel *et al*., 2010). Indeed in the present study, ground beetles were the only taxa to be influenced significantly at more than one spatial scale by the grazing state x altitude interaction. This may be explained by a 'spill-over' effect influencing highly mobile species, allowing them to take advantage of neighbouring farms (Hendrickx *et al*. 2009; Meyer *et al*., 2009). At the small scale, as well as vegetation structure and composition, soil factors and microclimate, habitat type, stone density and grazing intensity have been found to strongly influence ground beetle diversity and movement patterns (Negro *et al*., 2007; Gongalsky and Cividanes, 2008; Cole *et al*., 2010). Feeding groups have also been shown to differ with scale. Herbivorous insect assemblages were found to be affected by local habitat changes (influenced by management), while predatory assemblages were found to respond at the regional scale (Stoner and Joern, 2004). This highlights the importance of evaluating multiple spatial scales to incorporate different trophic levels. Spatial scale can affect trophic interactions by limiting the movements and handling times of resources and consumers, which will affect consumption rates (Schweiger *et al*., 2005; Van de Koppel *et al*., 2005; Gongalsky and Cividanes, 2008). The size of an organism will also determine the scale to which it best responds. Larger beetles were found to respond to their habitats at larger spatial scales (Holland *et al*., 2005; Schweiger *et al*., 2005), although elements, such as the proportion of woody elements in a landscape, will also determine the scale (Aviron *et al*., 2005). Small carabids, which are more mobile, were not found to respond to any factors, regardless of scale (Aviron *et al*., 2005). The availability of resources for carabids is unpredictable at the small scale, therefore a heterogeneous habitat may benefit carabids by providing a more uniform resource distribution (Niemelä *et al*., 1996). Small-scale landscape heterogeneity has also been shown to benefit carabid species composition (Weibull and Östman, 2003). Soil factors have been shown to influence more homogeneous sites, while vegetation structure influenced heterogeneous sites to a greater extent (Bossenbroek *et al*., 2005). Distribution of carabids at the small scale is thought to be determined by their ability to detect fine scale changes in habitat heterogeneity, while regional scale differences in habitat composition, geology and management history, are thought to explain carabid distribution at the large scale (Niemelä *et al*., 1992; Aviron *et al*., 2005; Gongalsky and Cividanes, 2008). Cole *et al*. (2010) found that at wider spatial scales, the amount of bracken and *Juncus* in the surrounding area were important factors influencing carabid assemblages. These vegetation types may be important for resting or hunting or they may be valuable sources of either low or high humidity, indicating the detection of a moisture gradient at a wide spatial scale (Cole *et al*., 2010).

The largest amount of variation in bird assemblage attributable to grazing management was observed at the smallest spatial scale (transect), while the largest amount of variation in bird assemblage attributable to altitudinal effects was observed at the medium spatial scale (habitat). Significant grazing state and altitude effects were found for birds at the farm scale, as well as for ground beetles. However, although birds perceive their landscape at a broader scale and are more mobile than plants or ground beetles (Bossenbroek *et al*., 2005), birds were not affected by the grazing state x altitude interaction at the largest scale (farm) in the present study. This may be because landscape characteristics, such as the proportion of grassland or hedge length, rather than farm management have been shown to drive bird abundance (Saab, 1999; Gabriel *et al*., 2010). It may also be due to the fact that perhaps this scale was not large enough to detect differences in bird assemblages and landscape comparisons may have been more appropriate. However, the measure used to study spatial scale is also important. Moreira *et al*. (2005) found that wintering bird *abundance* was influenced by factors at the field scale, while *species richness* was affected at the landscape level. Fletcher and Huto (2008) found that bird distribution was negatively affected by grazing at the local scale. Although moderate grazing regimes may help to create habitat mosaics, providing many resources, to support high invertebrate diversity and thus favouring upland bird species (Buchanan *et al*., 2006; Dennis *et al*., 2008). The spatial scale at which landscape may influence bird abundance has also been shown to vary with territory size or foraging home range (Söderström and Pärt, 2000).

Some researchers have found that more mobile taxa (birds and carabids), on average, had less similar communities at the field (small) and farm (medium) scale than plants (Flohre *et al*., 2011), under varying levels of agricultural intensification. In the present study grazing state alone (irrespective of altitude) did indicate this for ground beetle communities, where similarity was lowest at all spatial scales, however birds still had more similar communities than plants at all scales. This result may be explained by a possible homogenising effect of dispersal ability on bird species (Mouquet and Loreau, 2003; Cadotte, 2006). MacNally *et al*. (2004) found that the similarity of bird and butterfly species composition increased as spatial scale increased, as was found for all taxa in the present study. Here, many more plant species were found to contribute to the similarity of plant assemblages than beetle or bird species to their respective assemblages. The four most important plant species contributed an average of 42% similarity to assemblages influenced by grazing state, while the first four ground beetle species contributed an average of 68% and birds, 71%. Similarity also decreased as grazing intensity increased for plants and ground beetles. However, for bird assemblages, lightly-moderately grazed sites were the most similar and moderately grazed sites the least similar. Assemblages affected by altitude also saw four most important plant species contributing a lower average similarity than the first four ground beetle or bird species. The most obvious pattern with altitude was the very high degree of similarity in bird assemblages above 200m.

The contribution of grazing state and altitude to plant, ground beetle and bird assemblage across all spatial scales varied with taxon, which highlights the importance of considering traits such as mobility and size as part of agri-environment management. The optimum spatial scale at which to collect habitat variables will be influenced by several factors, such as the habitat requirements, range and mobility of the species under investigation and habitat heterogeneity, which will all vary from location to location (Cole *et al*., 2010; Flohre *et al*., 2011). As different taxa respond to their environment at different scales, as well as at multiple spatial scales (Gabriel *et al*., 2010), an environment which is sufficiently heterogeneous at all spatial scales will enable different taxa to find their own habitats (Pärt and Söderström, 1999). When aiming to maintain and enhance biodiversity through grazing management, knowledge of the importance and interaction of environmental factors, such as altitude, on the composition and function of plant, ground beetle and bird communities, across a range of spatial scales, is vital (Schweiger *et al*., 2005; Kohyani *et al*., 2008). By determining appropriate spatial scales for a species or group, management schemes could be established to aid in biodiversity conservation. Planting new hedgerows and increasing the amount of permanent grassland on a farm, as well as decreasing fertiliser, insecticide and herbicide use would be highly beneficial (Aviron *et al*., 2005). However, even when a specific grazing regime is in place, differences in the foraging behaviour of livestock may result in fine-scale variations in vegetation structure resulting in habitat mosaics containing even more resources (Dennis *et al*., 2002; Cole *et al*., 2010). Within-farm biodiversity is influenced by management at the individual farm level but also by the management of surrounding farms. Therefore, it been suggested that agri-environment schemes aim to manage spatial scale beyond the level of farm, by encouraging multiple farmers within a landscape to participate in single landscape-level benefiting schemes (Gabriel *et al*., 2010).

6.6 Conclusions

In understanding the scale of patterns in upland vegetation which affect flora and faunal diversity, grazing management decisions can be made which aim to maximise the biodiversity of as many taxa as possible. This study has shown that plant, ground beetle and bird assemblages are all influenced to different extents by management and environmental factors at different, as well as multiple scales. Further studies aimed at increasing the spatial scale of observation are recommended, particularly for birds.

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Chapter 7

General Discussion

Scottish Blackface ewe with lamb. (Photo: Roz Anderson).

7.1 Main findings

As the first study of its kind in Ireland, this project provided a detailed analysis of the influence of grazing management on the diversity of the Irish uplands, whilst also incorporating information from the lowlands of the hill sheep study farms. This thesis has addressed multiple components of biodiversity – plants, ground beetles and birds, at a hierarchy of scales, management regimes and altitudes and quantified a range of different effects on each of these groups.

TWINSPAN classified a continuum of vegetation types which differed in their grazing regime due to the dominance of particular plant species such as *Molinia caerulea* or *Nardus stricta*. NMS identified a soil gradient and a grazing management gradient in the plant assemblage data. Soil moisture and pH were particularly important in explaining variation, as were the variables vegetation height, % litter, signs of grazing (bitten leaves) and % dung. Many studies have also found that soil factors have a strong influence on plant species composition; particularly that of soil pH and moisture content (Power and Cooper, 1995; Ogutu, 1999; Lyon and Sagers, 2002; Lu *et al*., 2006; Huebner *et al*., 2007). Some have found that both environmental and grazing factors influence plant composition (Ejrnæs and Bruun, 2000; Reinhammar *et al*., 2002; Vandvik and Birks, 2002; Aerts *et al*., 2006).

The percentage of traditional ewes in a flock should be considered as part of a grazing management regime. At present, it appears that farms with 0% traditional ewes have adopted a grazing regime which results in low plant species richness below 300m but high plant species richness above 300m. Conversely, grazing management on farms with 100% traditional ewes yields high plant species diversity below 300m and low plant species richness above 300m. Farms with 70% traditional ewes exhibited similar plant species richness to farms with 0% traditional ewes, while farms with 50% traditional and 50% commercial ewes had very low overall plant species richness. As farms with this flock composition have the highest stocking rates (0.75 – 0.76 LU/ha) out of all four traditional ewe categories, it suggests that perhaps these farms are being overgrazed in the lowlands with the commercial ewes and overgrazed in the uplands with the traditional breeds. A major gap in the knowledge of the role of traditional breeds in farming systems exists (Wright *et al*., 2000; 2002), and with very few studies in the literature showing variations in the choices made by different sheep breeds (Osoro *et al*., 2002; Dumont *et al*., 2007), the findings of the present study perhaps provide a valuable contribution. Traditional sheep and cattle breeds are known to be less selective in their grazing behaviour than commercial breeds, allowing them to exploit low quality forage (Dumont *et al*., 2007), although this may be explained by differences in body size, dental and digestive anatomy (Illius and Gordon, 1987; Rook *et al*., 2004).

It appears that the ideal grazing regime for plant species richness on the Iveragh Peninsula involves a farm stocking rate of between 0.18 and 0.46 LU/ha (depending on type of habitats on farm) made up entirely of traditional breeds such a Scottish Blackface or Galway ewes. It is suggested that agri-environmental schemes therefore offer increased funding for traditional breeds in these areas and as stocking rates alone are believed to be a poor indication of grazing pressure in the uplands (Grant and Maxwell, 1988; Armstrong and Milne, 1995), the inclusion of percentage of traditional ewes may help address this dilemma.

However, the economic performance of traditional breeds is generally regarded as poorer due to marketing difficulties (Rook *et al*., 2006). Therefore, if a landowner preferred to keep a flock of 100% or 50% commercial ewes, then the grazing regime should strongly focus on the habitat types available for grazing on a farm and consider seasonal and rotational grazing, avoiding wet areas completely during the winter months, for example. Blanket bog, in particular, needs special consideration. Perhaps if a farm comprises a large percentage of undamaged blanket bog, whether upland or lowland, it should receive funding to preserve 'carbon storage' which should ultimately benefit carbon sequestration and limit climate change. However, it has been suggested that a reconnection with local culture and food networks may actually provide a market advantage for traditional breeds (Mills *et al*., 2007).

In the present study, farms with a small percentage of improved grassland in the lowlands tended to have a higher percentage of traditional ewes and graze the uplands for the majority of the year (Kramm *et al*., 2008; O'Rourke *et al*., 2012). This may explain the reason why above 300m farms with 100% traditional ewes have lower plant species richness, although across the whole farm plant species richness is the highest of any category. These farms perhaps comprise the lowest proportions of 'green land' or improved grassland. This highlights the key importance of habitat type in grazing management.

Plant biomass and vegetative cover are known to be good measures of ecosystem functioning (Naeem *et al*., 1995; Tilman *et al*., 1997; Allen-Diaz and Jackson, 2000; Schwartz *et al*., 2000). Plant species richness was found to have a positive effect on the percentage of vegetative cover, which may be viewed as a driver of the regulating ecosystem service of erosion control, owing to its direct influence on erosion rates (Busby *et al.*, 1994). Plant functional group richness and altitude were found to positively influence biomass, which may also be seen as a driver of the supporting ecosystem services of primary production and nutrient cycling, as litter decomposition is important in nutrient cycling and productivity (Scherer-Lorenzen, 2008). Functional diversity has been found to have a stronger impact on ecosystem processes than species diversity, hence focusing on functional groups may be key in the study of ecosystem functioning (Tilman *et al.*, 1997; Petchey and Gaston, 2002; Petchey *et al.*, 2004; Jiang *et al.*, 2007).

The use of ground beetle functional groups, as with plant functional groups, may also provide the best indicator of ecosystem functioning, particularly as the use of vegetation structure by ground beetles is highly dependent on their functional requirements (Butterfield *et al.*, 1995; Vanbergen *et al.*, 2005; Cole *et al.*, 2006). In fact plant functional diversity was found to be more important than plant species diversity for ground beetles in the present study.

Vegetation height and percentage of litter in the sward are important variables for ground beetles, particularly as they influence the microclimatic factors of humidity and temperature (Dennis *et al.*, 1998; Cole *et al.*, 2010; Williams and Gormally, 2010). Long vegetation also provided ideal conditions for large carabids to hide from predators. Soil moisture is also vital to ground beetles (Gardner, 1991; Rushton *et al.*, 1991; Lövei and Sunderland, 1996; Bhriain *et al.*, 2002; Dennis, 2003), and damp habitat types such as blanket bog provide valuable conditions for rare or threatened species such as *Carabus clatratus* (Williams and Gormally, 2010). This is particularly critical as carabids are known to be suffering especially serious biodiversity losses (Brooks *et al.*, 2012).

Grazing state and altitude were also important for ground beetles (Luff and Rushton, 1989; Luff *et al.*, 1989; Dennis *et al.*, 1997; Cole *et al.*, 2006; Maveety *et al.*, 2011). The short vegetation of wind-clipped montane heath was valuable for specialist predators which fed on Collembola and were dependent upon the use of visual cues for hunting. Again, this habitat type is vital for the small and isolated populations of high altitude specialists, such as *Notiophilus aesthuans*, which may be particularly vulnerable to environmental change (McCormack *et al.*, 2006). Classifying individual *habitats* with a particular grazing state, as opposed to whole *farms*, provided a more accurate explanation of beetle abundance. Below 200m a heavy level of grazing appeared to support the highest carabid, staphylinid and other beetle abundance, while between 200 and 600m, a moderate level of grazing was most beneficial. Above 600m a light level of grazing was preferable.

It appears that soil moisture and the % scrub on a farm may actually have been driving the observed effects of beetle abundance and species richness on the ecosystem service of soil organic carbon (SOC). When soil moisture was included in models, beetle abundance and species richness had a positive effect on SOC, without the inclusion of soil moisture, beetle abundance and species richness actually had a negative effect on SOC. Carabid evenness, however, did have a positive effect on SOC in its own. This highlights the importance of measurement choice and Magurran (1988) recommends measuring both species richness and evenness whenever possible, due to the fact that they can be influenced by different processes (Wilsey and Stirling, 2007). The % scrub had a positive influence on SOC under a heavy level of grazing but a negative influence under a light-moderate and light level of grazing, perhaps indicating that the presence of scrub on farms under heavier levels of grazing may buffer any negative effects of heavy grazing or trampling on SOC.

Carabid consumption rate was found to have a positive effect on SOC, but only under light-moderate and heavy levels of grazing. This shows that on lightly grazed sites carabid abundance and the % scrub actually have a negative effect on SOC. This may be explained by the reduction in organic inputs from manure (Post and Kwon, 2000; Milne, 2012) or perhaps lightly grazed sites contained very high proportions of woody plant species (scrub such as *Ulex* spp), which are known to decrease SOC (Post and Kwon, 2000). Unexpectedly, there was a rise in SOC with carabid abundance and the % scrub on heavily grazed sites, suggesting that perhaps the presence of carabid beetles is particularly important under a heavier level of grazing to counteract any negative effects of erosion which may lead to a reduction in SOC (Su *et al*., 2003; Worrall and Evans, 2009).

Altitude and habitat type appeared to be much more important than grazing state for birds, with altitude explaining almost three quarters of the variation in bird assemblage composition. In fact altitude is known to be central in explaining bird distributions (Debinski and Brussard, 1994). As with ground beetles, damp habitats, such as blanket bog are also important for waders such as snipe (Henderson *et al*., 2004). The percentage of upland blanket bog per farm had a positive effect on meadow pipit density. The percentage of scrub on a farm was also extremely important for bird density which was at its maximum on farms with 16% scrub. Indeed Nikolov (2010) recommends the inclusion of approximately 15% scrubland whenever possible and 15-20% shrub or hedgerow cover has also been advocated as being beneficial for birds (Woodhouse *et al.*, 2005; Brambilla *et al.*, 2007). Scrub provides shelter from bad weather and protection from predators. However it was found to have a high turnover rate in the present study, suggesting that it is a temporary stop for many species and indeed Fuller *et al.* (1999) found that no species are confined to scrub habitats alone. Improved grassland was found to exhibit the highest bird species turnover rate of any habitat in the study. Grassland sites are known to have higher bird species turnover than shrub dominated sites (Rotenberry and Wiens, 1980). This may be explained by the high percentage of dung in these habitats, providing a plentiful food supply for insectivorous and granivorous birds (Tucker, 1992; Wilson *et al.*, 1996; Yuan, 1996; Atkinson *et al.*, 2005). It may also be the result of smaller field sizes and consequent higher hedgerow densities experienced on Irish farms (Lysaght, 1989; Siriwardena *et al.*, 2000).

Although grazing state explained only 10-14% of the variation in bird species composition across the whole farm, it did explain 35 – 49% of the variation in bird species composition in the uplands (> 200m) across both years. The uplands may exhibit greater differences in bird assemblages as a result of grazing due to their wide open nature, perhaps indicating that mobile species such as birds respond better at this scale (Bossenbroek *et al.*, 2005). These open habitats are particularly important as 33% of open habitat bird species are in decline (Laiolo *et al.*, 2004) and the abandonment of grazing has indicated a fall in rare or threatened bird species (Verhulst *et al.*, 2004). In fact, most species of conservation concern in the present study, such as skylark, wheatear, starling or chough, were actually found on heavily grazed sites, highlighting the need for heterogeneous mosaics of short vegetation for ground feeding insectivores and open habitat species, such as meadow pipit, skylark or wheatear but also scrub patches and long vegetation for foliage insectivores and ground nesting species, which will also benefit from lower levels of trampling (Vickery *et al.*, 2001). A comparison of farms across the regional scale did, however, find a significant effect of grazing state on bird species richness, with lightly grazed sites exhibiting the highest bird species richness in both years. The grazing effect at a larger scale again, may be explained by the high mobility of birds (Bossenbroek *et al.*, 2005).

The greatest difference in bird species turnover (beta diversity) between the uplands and lowlands was found in lightly grazed sites, with the uplands of these sites exhibiting very low species turnover. Perhaps this may be an indication of abandonment of these areas, or it may reflect an increase in stability. A low percentage of bare ground and a high percentage of vegetation litter were found to benefit birds. Bare ground is known to be important for birds (Moreira, 1999). A high percentage of forbs and plant species richness on a site resulted in high bird evenness but low species turnover, suggesting that high plant diversity may have a stabilising effect on birds, as observed on moderately grazed sites. In fact habitat heterogeneity is known to provide a stabilising effect on bird communities (Devictor and Jiguet, 2007). Forbs are a good indicator of grazing state (Dumont *et al*., 2009) and plant species richness has been found to influence the choice of foraging area by birds (Alder and Marsden, 2010). Bird species turnover was found to be lower on sites with a high percentage of moisture in the soil. Perhaps wet areas are home to a greater abundance of invertebrates, providing a stable food resource for insectivorous bird species (Buchanan *et al*., 2006; Jankowski *et al*., 2009). The use of bird functional groups, as with ground beetle and plant functional groups, may also be a valuable indicator of ecosystem functioning. Ground feeding insectivores were most common on heavily or moderately grazed sites, while foliage feeding insectivores were generally only found in lightly grazed sites. Others have also found an effect of grazing on insectivorous birds (Fuller and Gough, 1999; Henderson *et al*., 2004; Atkinson *et al*., 2005). Omnivores and scavengers were found in equal numbers across all grazing states and scavengers in equal numbers in the uplands and lowlands, while granivore numbers in the uplands were relatively low.

An ideal environment should be sufficiently heterogeneous at all spatial scales but not fragmented, which is often the case on mountains (Poore, 1992; Haslett, 1997). As grazing intensity increased, in the present study, the similarity of plant and ground beetle assemblages decreased, indicating that perhaps there was greater structural heterogeneity on heavily grazed sites than lightly grazed sites. Moderately grazed sites exhibited the lowest similarity for bird assemblages. When examining altitudinal effects, variation in plant assemblage was greatest at the smallest spatial scale (quadrat), while the effects of grazing state exhibited the greatest variation in plant assemblage at the largest spatial scale (farm). This highlights the importance of choosing a spatial scale which best reflects the taxa and variables of interest. Particularly as the scale of measurement will vary with the size, mobility and life history of the chosen species/ group (Pärt and Söderström, 1999; Cole *et al*., 2010; Gabriel *et al*., 2010).

7.2 Management implications

The management history of a site may determine the extent to which an area will change under various grazing regimes, so it is extremely important to record factors such as the length of time a particular area has been grazed (**Fig. 7.1**). It is also valuable to note any environmental designations, such as SACs. If the uplands of the site are part of a commonage then other landowners must be consulted prior to any management decisions being taken. If the site is presently under any agri-environmental schemes, those should be carefully considered. All habitats on the farm should be mapped and their areas recorded. Previous studies have highlighted the importance of farm hedgerow length (Copland and O'Halloran, 2010), so an estimation of total farm hedgerow length along with treelines, stone walls and farm buildings is highly recommended. The altitude and slope (determining potential risk of erosion) at each survey point (e.g. quadrat) should be recorded and a rough estimation of soil/ habitat moisture should be taken, perhaps by creating a simple 'degree of softness underfoot' scale. Climatic conditions such as annual rainfall or temperature for an area should be considered. At least 15% scrub is recommended per farm and the percentage of improved grassland may help to determine the length of upland grazing season. The sheep stocking rate (LU/ha) per farm and the percentage of traditional ewes in the flock may be attained from the landowner and may be used in conjunction to manage particular habitat types differing in forage quality. It is vital to achieve a record of the impact of the present grazing regime upon the vegetation before any changes are made as part of the baseline data. This may be undertaken using a quadrat of perhaps 2m x 2m and recording factors such as vegetation height, % litter, % dung, % bare ground, % leaves that have been bitten and % indicator species such as *Molinia caerulea* or *Nardus stricta*. MacDonald *et al*. (1998) provide a valuable guide to surveying land management impacts in the uplands. It is advisable to also estimate the condition of the land surrounding the study farm. The taxa or species of interest should be identified and knowledge of their size, mobility and life history will help inform the appropriate scale of measurement, as well as the type of measurement, such as density or species richness, for example. It may be preferable to focus on functional groups such as graminoids, forbs or shrubs for plants, generalist predators, specialist predators or phytophages for ground beetles or insectivores, granivores, scavengers or omnivores for birds. A site-specific grazing regime may then be devised incorporating particular stocking rates (dependent upon the percentage of traditional ewes in the flock), the proportion of different habitat types present on the farm and the most appropriate season to graze particular habitats. It is then imperative that the effects of the grazing regime on the vegetation, measurements of biodiversity and productivity of the farm are monitored on a regular basis.

It is important that stocking rates are not static throughout the year, as this could lead to overgrazing in the winter, when there is little growth and undergrazing in the summer months (Ebrahimi *et al*., 2010). It must also be remembered that vegetation in the uplands will grow more slowly under the cooler temperatures. Habitat-specific stocking rates are recommended, such as 0.4 LU/ha for acid grassland (Gotts and MacKintosh, 1996). Blanket bog would require a much lower stocking rate and perhaps complete exclusion from grazing during the winter months. In fact, the timing of grazing is vital. Early spring grazing may be used to control coarse grasses such as *Nardus stricta*, which become unpalatable later in the year. A reduced stocking rate in late spring should decrease the trampling of the eggs of ground nesting birds, while a low summer stocking rate should enable plants to flower and set seed. Increased stocking rates in autumn will keep swards short (Gotts and MacKintosh, 1996).

It is crucial to manage spatial scale beyond that of the farm unit and the encouragement of multiple landowners to participate in single landscape-level benefiting schemes are recommended (Gabriel *et al*., 2010). It has been shown, for example, that financial support through agri-environment measures has a positive impact on cooperation between landowners, which in turn has a beneficial effect on the conservation of commonage (uplands held under common property in Ireland) (Di Falco and Rensburg, 2008).

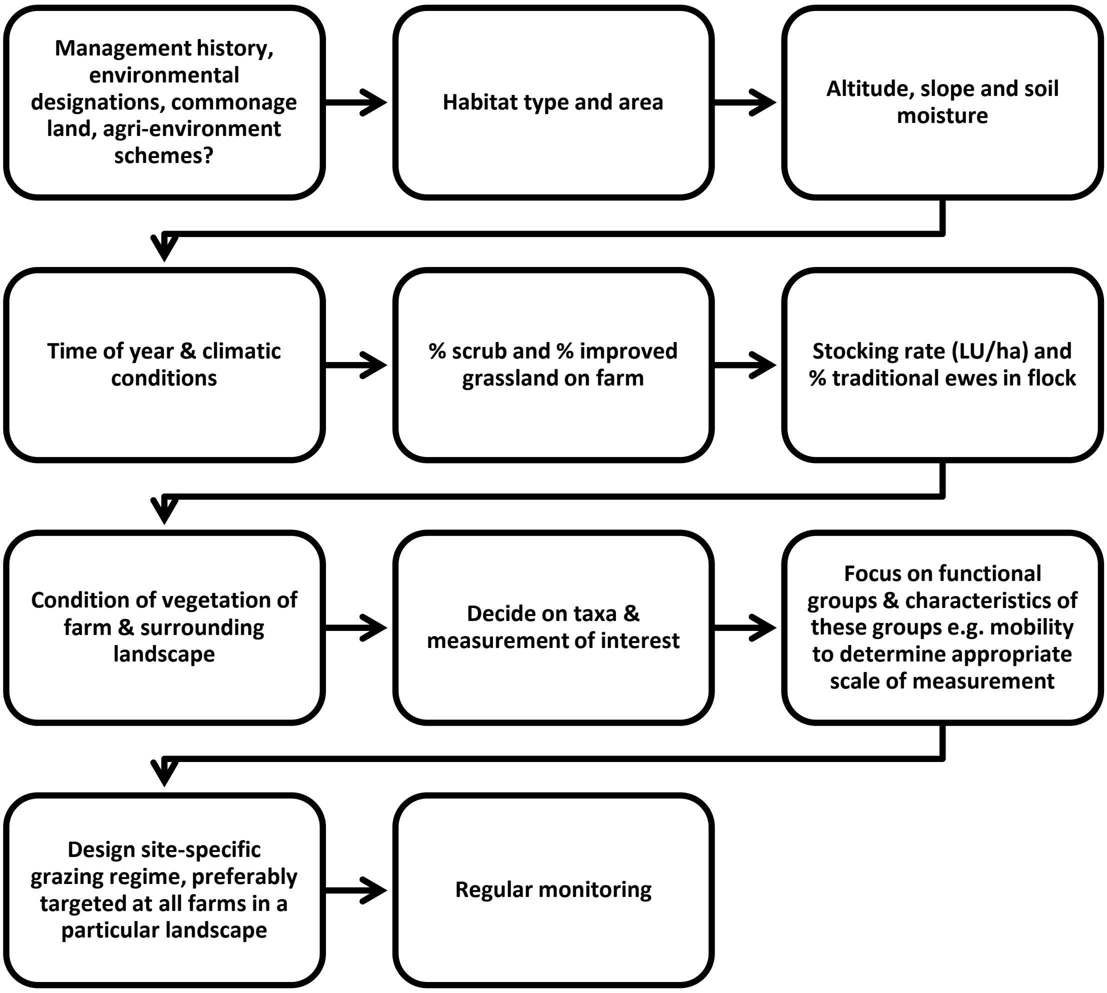

Fig. 7.1 Suggested stages in the assessment of a site for implementation of a grazing management regime (incorporating key findings from the present study).

7.3 Future considerations

EU agri-environment schemes are one of the most important mechanisms by which public goods or ecosystem services are protected through payments to manage the rural environment, mainly through biodiversity objectives (Finn and Ó hUallacháin, 2011). It is important that the effectiveness of these schemes are evaluated in order to satisfy EU agri-environmental legislation and demonstrate value for money to taxpayers. The Rural Environment Protection Scheme (REPS) was initiated in Ireland in 1994. However, to date there is insufficient evidence with which to judge the effectiveness of this scheme at a national scale (Finn and Ó hUallacháin, 2011). It is recommended that a national scale assessment of the scheme be undertaken, which will help in gauging the performance of the new Agri-Environment Options Scheme (AEOS), implemented in 2010.

An increase in the number of study farms across the Iveragh Peninsula would enable the spatial scale of observations to be increased to that of the landscape, which may hopefully provide further information on many taxa, particularly birds and other highly mobile species (Bossenbroek *et al*., 2005). Further analysis of habitat diversity surrounding individual quadrats, pitfall traps and transects at different spatial scales, using different sized buffer zones (Müller *et al*., 2004), (across farm boundaries) may also prove extremely useful, particularly in the analysis of landscape complexity and habitat fragmentation (Davies and Margules, 1998; Fuhlendorf and Smeins, 1999; Austrheim and Eriksson, 2001; Kinnunen *et al*., 2001; Olff and Ritchie, 2002).

Some carabid species have shown a significant preference for *Calliphora* blowfly larvae (Mair and Port, 2001) and as blowfly strike is the most prevalent ectoparasite-mediated disease to affect sheep in the UK and northern Europe (Snoep *et al*., 2002; Bisdorff and Wall, 2008), this would form an extremely valuable line of research, particularly as current climate change scenarios predict an elongated blowfly season with earlier spring emergence and a higher incidence of fly strike (Taylor, 2012). The use of a biological control agent, such as the ground beetle, would enable a decrease on the reliance on insecticides (Tellam and Bowles, 1997). Granivorous and omnivorous carabids have also been shown to regulate the abundance of weed species in the seedbank (Bohan *et al*., 2011). This may be valuable in some upland areas where the unpalatable grass, *Nardus stricta*, dominates. Carabids have also been shown to be successful in controlling slugs (Asteraki, 1993; Oberholzer and Frank, 2003; Tulli *et al*., 2009) and carabid beetle larvae have been found to consume the eggs of the heather beetle pest (Peterson *et al*., 2004).

7.4 Conclusions

This study has shown that grazing management can be used to influence plant, ground beetle and bird diversity, assemblages and functional groups across varying altitudes, habitats and spatial scales. It is imperative that we understand the way in which grazing management influences biodiversity in order for national governments to respond to changes in EU agricultural policy (Pienkowski *et al*., 1996). In adopting a grazing management regime, it is essential that ecological factors are considered alongside social and economic issues and vital that species-rich farmland is not maintained simply by the promotion of rural poverty (McCracken *et al*., 1997). A mosaic of different habitats under varying levels of grazing management, across a range of spatial scales, should provide enough variation to attract as many different species and functional groups as possible (Milne, 1996). The landscape must be regarded as an integral unit, regardless of ownership or past management practices (Cobb *et al*., 1999). The key link between policy and conservation management of upland areas is grazing pressure (Hanley *et al*., 2008) and the successful use of grazing management in agri-environment schemes aimed at enhancing biodiversity, lies in site-specific planning in conjunction with local conditions, residents and land managers (Brown and Stillman, 1993; Marriott *et al*., 2004; Edwards, 2005; Bracken and Bolger, 2006; Metera *et al*., 2010). Preventing the deterioration of the mountains, their valuable species and habitats and the loss of an ancient way of life will depend on conservationists, landowners and policy makers working together to improve management practices. Only then will these remarkable places be able to survive and flourish for future generations.

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Appendix A

S2.1 Ordination axes and corresponding significant correlations for variables and data sets.

Data set	Habitat/environmental variable	Ordination axis	Correlation	P
All	Alt:state	1	$r_s = 0.239$	$p = 0.004$
		2	$r_s = -0.441$	$p < 0.0001$
	State (farm scale)	2	$r_s = -0.539$	$p < 0.0001$
	State (habitat scale)	2	$r_s = -0.585$	$p < 0.0001$
	TWINSPAN group	1	$r_s = -0.815$	$p < 0.0001$
		2	$r_s = -0.356$	$p < 0.0001$
	Habitat type	1	$r_s = 0.473$	$p < 0.0001$
		2	$r_s = 0.395$	$p < 0.0001$
		3	$r_s = 0.225$	$p = 0.007$
	Altitude	1	$r_s = 0.445$	$p < 0.0001$
		2	$r_s = 0.288$	$p < 0.0001$
	Drainage	1	$r_s = 0.737$	$p < 0.0001$
		3	$r_s = -0.365$	$p < 0.0001$
	Firmness	1	$r_s = 0.736$	$p < 0.0001$
		2	$r_s = 0.170$	$p = 0.042$
		3	$r_s = -0.327$	$p < 0.0001$
	Slope	1	$r_s = -0.177$	$p = 0.033$
		2	$r_s = -0.194$	$p = 0.002$
		3	$r_s = 0.255$	$p = 0.002$
	Vegetation height	2	$r_s = 0.598$	$p < 0.0001$
		3	$r_s = -0.168$	$p < 0.0001$
	Soil depth	1	$r_s = 0.590$	$p < 0.0001$
		2	$r_s = 0.229$	$p = 0.006$
		3	$r_s = -0.421$	$p < 0.0001$
	Soil pH	1	$r_s = -0.650$	$p < 0.0001$
	Soil nitrogen	1	$r_s = 0.660$	$p < 0.0001$
		2	$r_s = -0.386$	$p < 0.0001$
	Soil carbon	1	$r_s = 0.215$	$p = 0.01$
		2	$r_s = -0.355$	$p < 0.0001$
	Soil phosphorus	1	$r_s = 0.409$	$p < 0.0001$
	Soil moisture	1	$r_s = -0.720$	$p < 0.0001$
		2	$r_s = 0.210$	$p = 0.011$
	% Moss	1	$r_s = 0.466$	$p < 0.0001$
		2	$r_s = 0.186$	$p = 0.026$
		3	$r_s = 0.176$	$p = 0.035$
	% Rock	1	$r_s = -0.324$	$p < 0.0001$
		3	$r_s = 0.198$	$p = 0.017$
	% Bare ground	1	$r_s = 0.244$	$p = 0.003$
	% Dung	1	$r_s = -0.172$	$p = 0.040$
		2	$r_s = -0.565$	$p < 0.0001$
	% Vegetation litter	2	$r_s = 0.459$	$p < 0.0001$
	% Signs of grazing	1	$r_s = -0.376$	$p < 0.0001$
		2	$r_s = -0.584$	$p < 0.0001$
	% Grass	1	$r_s = -0.602$	$p < 0.0001$
		2	$r_s = -0.421$	$p < 0.0001$
	% Forbs	1	$r_s = -0.562$	$p < 0.0001$
	% Sedges	1	$r_s = 0.429$	$p < 0.0001$
		2	$r_s = -0.225$	$p = 0.007$
		3	$r_s = -0.221$	$p = 0.008$
	% Shrubs	1	$r_s = 0.690$	$p < 0.0001$
		2	$r_s = 0.311$	$p < 0.0001$

	3	$r_s = 0.165$	$p = 0.048$
% Rushes	1	$r_s = 0.286$	$p = 0.001$
	2	$r_s = -0.201$	$p = 0.016$
	3	$r_s = -0.281$	$p = 0.001$
Plant diversity	2	$r_s = -0.283$	$p = 0.001$
Plant species richness	1	$r_s = -0.218$	$p = 0.009$
	2	$r_s = -0.288$	$p < 0.0001$
Plant evenness	1	$r_s = 0.265$	$p = 0.001$
	2	$r_s = 0.187$	$p = 0.025$
Habitat diversity	2	$r_s = 0.358$	$p < 0.0001$
	3	$r_s = 0.176$	$p = 0.035$
Habitat richness	2	$r_s = 0.214$	$p = 0.01$
	3	$r_s = 0.256$	$p = 0.002$
Habitat evenness	3	$r_s = -0.256$	$p = 0.002$
% Wet heath	3	$r_s = 0.239$	$p = 0.004$
% Upland blanket bog	2	$r_s = -0.329$	$p < 0.0001$
% Lowland blanket bog	2	$r_s = 0.202$	$p = 0.015$
	3	$r_s = -0.289$	$p < 0.0001$
% Dry-humid acid grassland	3	$r_s = -0.314$	$p < 0.0001$

S2.2 Ordination axes and corresponding significant correlations for variables and data sets in the lowlands.

Data set	Habitat/environmental variable	Ordination axis	Correlation	P
Lowlands	Alt:state	2	$r_s = 0.413$	$p < 0.0001$
	State (farmscale)	2	$r_s = 0.413$	$p < 0.0001$
	State (habitatscale)	2	$r_s = 0.363$	$p = 0.002$
		3	$r_s = -0.281$	$p = 0.019$
	TWINSPAN group	1	$r_s = 0.843$	$p < 0.0001$
		2	$r_s = 0.425$	$p < 0.0001$
		3	$r_s = 0.260$	$p = 0.031$
	Habitat type	1	$r_s = -0.648$	$p < 0.0001$
		2	$r_s = -0.629$	$p < 0.0001$
	Altitude	2	$r_s = -0.275$	$p = 0.022$
	Aspect	1	$r_s = 0.308$	$p = 0.01$
	Drainage	1	$r_s = -0.738$	$p < 0.0001$
	Firmness	1	$r_s = -0.702$	$p < 0.0001$
	Slope	1	$r_s = 0.388$	$p = 0.001$
		1	$r_s = -0.259$	$p = 0.031$
	Vegetation height	2	$r_s = -0.486$	p 0.0001
	Soil depth	1	$r_s = -0.623$	$p < 0.0001$
	Soil pH	1	$r_s = 0.723$	$p < 0.0001$
	Soil nitrogen	1	$r_s = -0.741$	$p < 0.0001$
	Soil carbon	1	$r_s = -0.432$	$p < 0.0001$
	Soil phosphorus	1	$r_s = -0.370$	$p = 0.002$
	Soil moisture	1	$r_s = 0.742$	$p < 0.0001$
	% Moss	1	$r_s = -0.335$	$p = 0.005$
	% Rock	1	$r_s = 0.255$	$p = 0.035$
	% Bare ground	1	$r_s = -0.406$	$p = 0.001$
		2	$r_s = -0.293$	$p = 0.015$
	% Dung	1	$r_s = 0.288$	$p < 0.016$
		2	$r_s = 0.541$	$p < 0.0001$
		3	$r_s = -0.267$	$p = 0.027$
	% Vegetation litter	2	$r_s = -0.295$	$p = 0.014$
	% Signs of grazing	1	$r_s = 0.392$	$p = 0.001$
		2	$r_s = 0.570$	$p < 0.0001$
	% Grass	1	$r_s = 0.344$	$p = 0.004$
		2	$r_s = 0.522$	$p < 0.0001$
	% Forbs	1	$r_s = 0.684$	$p < 0.0001$
	% Sedges	1	$r_s = -0.383$	$p = 0.001$
	% Shrubs	1	$r_s = -0.720$	$p < 0.0001$
		2	$r_s = -0.414$	$p < 0.0001$
	Plant diversity	1	$r_s = 0.265$	$p = 0.028$
		2	$r_s = 0.298$	$p = 0.013$
	Plant species richness	2	$r_s = 0.263$	$p = 0.029$
	Habitat diversity	2	$r_s = -0.266$	$p = 0.027$
	% Scrub	3	$r_s = 0.293$	$p = 0.015$
	% Upland blanket bog	2	$r_s = 0.366$	$p = 0.002$
	% Lowland blanket bog	3	$r_s = 0.261$	$p = 0.03$
	% Improved grassland	1	$r_s = 0.292$	$p = 0.015$

S2.3 Ordination axes and corresponding significant correlations for variables and data sets in the uplands.

Data set	Habitat/environmental variable	Ordination axis	Correlation	P
Uplands	Alt:state	3	$r_s = -0.477$	$p < 0.0001$
	State (farmscale)	3	$r_s = -0.477$	$p < 0.0001$
	State (habitatscale)	3	$r_s = -0.602$	$p < 0.0001$
	TWINSPAN group	1	$r_s = 0.285$	$p = 0.013$
		3	$r_s = -0.8$	$p < 0.0001$
	Habitat type	2	$r_s = -0.621$	$p < 0.0001$
		3	$r_s = 0.527$	$p < 0.0001$
	Altitude	2	$r_s = -0.495$	$p < 0.0001$
		3	$r_s = 0.391$	$p = 0.001$
	Aspect	2	$r_s = 0.305$	$p = 0.008$
	Drainage	1	$r_s = -0.624$	$p < 0.0001$
		2	$r_s = 0.391$	$p = 0.001$
		3	$r_s = 0.348$	$p = 0.002$
	Firmness	1	$r_s = -0.515$	$p < 0.0001$
		2	$r_s = 0.365$	$p = 0.001$
		3	$r_s = 0.477$	$p < 0.0001$
	Slope	1	$r_s = 0.259$	$p = 0.025$
		3	$r_s = -0.305$	$p = 0.008$
	Vegetation height	2	$r_s = 0.412$	$p < 0.0001$
		3	$r_s = 0.271$	$p = 0.019$
	Soil depth	1	$r_s = -0.480$	$p < 0.0001$
		2	$r_s = 0.367$	$p = 0.001$
		3	$r_s = 0.407$	$p < 0.0001$
	Soil pH	1	$r_s = 0.397$	$p < 0.0001$
		2	$r_s = 0.336$	$p = 0.003$
		3	$r_s = -0.459$	$p < 0.0001$
	Soil nitrogen	1	$r_s = -0.669$	$p < 0.0001$
	Soil carbon	1	$r_s = -0.435$	$p < 0.0001$
	Soil phosphorus	2	$r_s = -0.255$	$p < 0.027$
		3	$r_s = 0.501$	$p < 0.0001$
	Soil moisture	1	$r_s = 0.472$	$p < 0.0001$
		3	$r_s = -0.495$	$p < 0.0001$
	% Moss	3	$r_s = 0.699$	$p < 0.0001$
	% Rock	1	$r_s = 0.320$	$p = 0.005$
		3	$r_s = -0.309$	$p < 0.007$
	% Bare ground	1	$r_s = -0.265$	$p = 0.022$
	% Dung	2	$r_s = -0.248$	$p = 0.032$
		3	$r_s = -0.366$	$p = 0.001$
	% Vegetation litter	1	$r_s = 0.314$	$p = 0.006$
		2	$r_s = 0.373$	$p = 0.001$
	% Signs of grazing	3	$r_s = -0.703$	$p < 0.0001$
	% Grass	3	$r_s = -0.614$	$p < 0.0001$
	% Forbs	1	$r_s = 0.319$	$p = 0.005$
		2	$r_s = 0.409$	$p < 0.0001$
		3	$r_s = -0.388$	$p = 0.001$
	% Sedges	1	$r_s = -0.443$	$p < 0.0001$
		1	$r_s = -0.225$	$p = 0.007$
		1	$r_s = -0.221$	$p = 0.008$
	% Shrubs	2	$r_s = -0.319$	$p = 0.005$
		3	$r_s = 0.774$	$p < 0.0001$
	% Rushes	1	$r_s = -0.489$	$p < 0.0001$
		2	$r_s = 0.419$	$p < 0.0001$
	Plant diversity	3	$r_s = -0.306$	$p = 0.007$
	Plant species richness	3	$r_s = -0.443$	$p < 0.0001$

Plant evenness	3	$r_s = 0.412$	$p < 0.0001$
Habitat diversity	3	$r_s = 0.478$	$p < 0.0001$
Habitat richness	3	$r_s = 0.286$	$p = 0.013$
Habitat evenness	1	$r_s = -0.237$	$p = 0.041$
% Scrub	1	$r_s = -0.297$	$p = 0.01$
% Wet heath	1	$r_s = 0.436$	$p < 0.0001$
	3	$r_s = 0.305$	$p = 0.008$
% Upland blanket bog	3	$r_s = -0.254$	$p = 0.028$
% Lowland blanket bog	1	$r_s = -0.362$	$p = 0.001$
	2	$r_s = 0.301$	$p = 0.009$
% Dry-humid acid grassland	1	$r_s = -0.350$	$p = 0.002$
	3	$r_s = -0.344$	$p = 0.003$
	1	$r_s = -0.458$	$p < 0.0001$
% Improved grassland	2	$r_s = 0.359$	$p = 0.002$

S2.4 Individual plant species significant correlations for all data.

Data set	Plant species	Ordination axis	Correlation	P
All	*Trifolium repens*	1	r_s = -0.349	p = 0.04
	Holcus lanatus	1	r_s = -0.504	p = 0.001
		2	r_s = -0.432	p = 0.005
	Cerastium semidecandrum	3	r_s = 0.645	p = 0.007
	Agrostis capillaris	1	r_s = -0.611	p < 0.0001
	Festuca vivipara	1	r_s = -0.540	p = 0.004
	Agrostis stolonifera	1	r_s = -0.397	p = 0.001
	Agrostis canina	1	r_s = -0.718	p < 0.0001
	Galium saxatile	2	r_s = -0.416	p < 0.012
	Ulex gallii	2	r_s = 0.547	p = 0.004
	Carex nigra	3	r_s = 0.541	p = 0.046
	Pteridium aquilinum	3	r_s = 0.725	p = 0.005
	Potentilla erecta	3	r_s = 0.269	p = 0.006
	Molina caerulea	2	r_s = 0.740	p < 0.0001
		3	r_s = -0.258	p = 0.021
	Nardus stricta	2	r_s = -0.470	p < 0.0001
		3	r_s = -0.479	p < 0.0001
	Juncus squarrosus	1	r_s = 0.341	p = 0.036
		2	r_s = 0.325	p = 0.046
	Vaccinium myrtillus	1	r_s = 0.637	p = 0.014
	Erica cinerea	3	r_s = 0.581	p < 0.0001
	Carex distans	3	r_s = -0.628	p = 0.009
	Calluna vulgaris	3	r_s = 0.611	p < 0.0001
	Trichophorum caespitosum	1	r_s = 0.379	p < 0.009
		3	r_s = -0.615	p < 0.0001
	Narthecium ossifragum	1	r_s = 0.366	p = 0.012
	Eriophorum angustifolium	2	r_s = 0.361	p = 0.014
		3	r_s = -0.431	p = 0.003
		1	r_s = 0.498	p < 0.0001
		2	r_s = 0.318	p = 0.012
	Erica tetralix			

S2.5 Individual plant species significant correlations for all data in the lowlands.

Data set	Plant species	Ordination axis	Correlation	P
Lowlands	*Ranunculus repens*	3	r_s = -0.697	p = 0.012
	Cerastium fontanum	3	r_s = -0.620	p = 0.010
	Holcus lanatus	2	r_s = 0.637	p < 0.0001
	Agrostis capillaris	2	r_s = 0.615	p = 0.015
	Festuca vivipara	1	r_s = 0.635	p = 0.02
		3	r_s = -0.575	p = 0.04
	Agrostis stolonifera	1	r_s = 0.349	p = 0.04
	Agrostis canina	1	r_s = 0.504	p = 0.004
	Ulex gallii	1	r_s = -0.646	p = 0.004
		2	r_s = -0.641	p = 0.004
	Potentilla erecta	2	r_s = -0.455	p = 0.002
	Molina caerulea	2	r_s = -0.558	p < 0.0001
		3	r_s = 0.520	p < 0.0001
	Nardus stricta	2	r_s = 0.656	p = 0.011
	Narthecium ossifragum	3	r_s = 0.654	p = 0.011
	Erica tetralix	1	r_s = -0.696	p < 0.0001

S2.6 Individual plant species significant correlations for all data in the uplands.

Data set	Plant species	Ordination axis	Correlation	P
Uplands	*Trifolium repens*	1	$r_s = 0.725$	$p = 0.027$
		3	$r_s = -0.725$	$p = 0.027$
	Cerastium fontanum	2	$r_s = 0.682$	$p = 0.021$
	Holcus lanatus	1	$r_s = 0.748$	$p = 0.008$
		3	$r_s = -0.642$	$p = 0.033$
	Agrostis capillaris	3	$r_s = -0.720$	$p = 0.002$
	Agrostis stolonifera	1	$r_s = 0.366$	$p = 0.028$
	Agrostis canina	2	$r_s = 0.525$	$p = 0.03$
	Carex echinata	3	$r_s = 0.866$	$p = 0.005$
	Potentilla erecta	1	$r_s = 0.272$	$p = 0.034$
	Molina caerulea	2	$r_s = 0.679$	$p < 0.0001$
	Nardus stricta	1	$r_s = -0.514$	$p < 0.0001$
		3	$r_s = -0.346$	$p = 0.022$
	Juncus squarrosus	2	$r_s = 0.504$	$p = 0.007$
	Vaccinium myrtillus	3	$r_s = 0.687$	$p = 0.007$
	Erica cinerea	2	$r_s = -0.703$	$p < 0.0001$
	Calluna vulgaris	1	$r_s = 0.349$	$p = 0.006$
		2	$r_s = -0.372$	$p = 0.003$
		3	$r_s = 0.556$	$p < 0.0001$
	Narthecium ossifragum	2	$r_s = 0.572$	$p = 0.011$
	Erica tetralix	2	$r_s = 0.365$	$p = 0.029$

S2.7 Three schemes: White and Doyle (1982), Fossit (2000) and Rodwell *et al*. (2000), which selected similar plant community classifications, enabling the prediction of the present management adopted.

TWINSPAN group	White & Doyle (1982) (Braun-Blanquet)	Fossitt (2000)	NVC (Rodwell *et al*., 2000)	Plant community and management description
A1	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Associations*: Cirsio-Molinietum* (NVC: M24), *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)) and *Hylocomio-Centaureetum nigrae* (NVC: U4(d), CG11(b), CG10(a))	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11), Dry calcareous & neutral grassland (Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6) and Improved agricultural grassland (Order: *Polygono arenastri-Poetalia annuae*, NVC: MG7)	MG10: *Holcus lanatus-Juncus effusus* rush-pasture, MG5: *Cynosurus cristatus-Centaurea nigra* grassland, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, CG10: *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland	Lowland unimproved grassland on upland margins, enclosed fields, maintained by grazing. Low grazing level suggested by high cover of *Holcus lanatus* and presence of *Ulex spp*. Combined with mosaic of good quality, nutritious upland sheep pastures under moderate grazing intensity (evidence: lack of *Nardus stricta*).
A2	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Associations: *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Nardo-Caricetum binervis* (NVC: U4(d), CG11(b), U5) and *Hylocomio-Centaureetum nigrae* (NVC: U4(d), CG11(b), CG10(a))	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11), Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6) and Improved agricultural grassland (Order: *Polygono arenastri-Poetalia annuae*, NVC: MG7)	MG5: *Cynosurus cristatus-Centaurea nigra* grassland, MG10: *Holcus lanatus-Juncus effusus* rush-pasture, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, CG10: *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland	Lowland unimproved grassland on upland margins, enclosed fields, maintained by grazing. Low grazing level suggested by high cover of *Holcus lanatus*. High cover of *Cynosurus cristatus* suggests previous re-seeding or application of artificial fertiliser. Combined with mosaic of good quality, nutritious upland sheep pastures under moderately high grazing intensity (evidence: presence of *Nardus stricta*).
A3	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Alliance: *Agropyro-rumicion crispi* (NVC: SM28, MG11-MG13, SD17, OV28, OV29), Associations: *Senecioni-Juncetum acutiflori* (NVC: M22(b), M22, M24(b)), *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Lolio-Plantaginetum* (NVC: MG7, OV21-OV23) and *Caricetum nigrae* (NVC: M7?)	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11), Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6) and Improved agricultural grassland (Order: *Polygono arenastri-Poetalia annuae*, NVC: MG7)	MG10: *Holcus lanatus-Juncus effusus* rush-pasture, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, CG10: *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland	Damp lowland unimproved grassland on upland margins, species-poor, enclosed fields, maintained by grazing. Combined with mosaic of good quality, nutritious upland sheep pastures under low grazing intensity (evidence: lack of *Nardus stricta* and presence of *Calluna vulgaris*). Some grazing present as the nutrient-loving (sheep dung & urine) *Festuca ovina*, and *Agrostis spp*. are present.
A4	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Alliance: *Agropyro-rumicion crispi* (NVC: SM28, MG11-MG13, SD17, OV28, OV29), Associations: *Senecioni-Juncetum acutiflori* (NVC: M22(b), M22, M24(b)), *Filipendulo-Iridetum pseudacori* (NVC: M28), *Lolio-Cynosuretum* (NVC: MG6), *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)) and Sub-association: *Centaureo-Cynosuretum juncetosum* (NVC: MG4, MG5(a), MG5)	Wet grassland (Order: *Molinietalia caeruleae* (*Junco conglomerati-Molinion*, NVC: M24, M25 and *Juncion acutiflori*, NVC: M23), Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6), Improved agricultural grassland (Order: *Polygono arenastri-Poetalia annuae*, NVC: MG7) and Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11)	MG10: *Holcus lanatus-Juncus effusus* rush-pasture, MG5: *Cynosurus cristatus-Centaurea nigra* grassland, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, CG10: *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland, M23: *Juncus effusus/acutiflorus-Galium palustre* rush-pasture	Damp lowland unimproved grassland on upland margins, enclosed fields, maintained by grazing. Presence of *Lolium perenne* suggests previous re-seeding or application of artificial fertiliser. Rushes such as *Juncus effusus* and *J. articulatus*, as well as species such as *Cirsium palustre*, *Rumex acetosa*, *Ranunculus repens* and *Poa trivialis* suggest a more heavily grazed sub-community (M23(b)). Combined with mosaic of good quality, nutritious upland sheep pastures under moderate grazing intensity (evidence: lack of *Nardus stricta* and presence of *Festuca ovina*, and *Agrostis spp*.).

A5	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Alliance: *Agropyro-rumicion crispi* (NVC: SM28, MG11-MG13, SD17, OV28, OV29), Associations: *Cirsio-Molinietum* (NVC: M24), *Centaureo-Cynosuretum* (NVC: MG5, MG5(a), MG5(c)), *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Nardo-Caricetum binervis* (NVC: U4(d), CG11(b), U5) and *Hylocomio-Centaureetum nigrae* (NVC: U4(d), CG11(b), CG10(a))	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11), Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6) and Improved agricultural grassland (Order: *Polygono arenastri-Poetalia annuae*, NVC: MG7)	MG5: *Cynosurus cristatus-Centaurea nigra* grassland, MG10: *Holcus lanatus-Juncus effusus* rush-pasture, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, CG10: *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland, M25: *Molinia caerulea-Potentilla erecta* mire, H7: *Calluna vulgaris-Scilla verna* heath	Lowland unimproved grassland on upland margins, enclosed fields, maintained by grazing. Moderate grazing level suggested by intermediate cover of *Holcus lanatus* and presence of *Ulex spp*. Combined with mosaic of good quality, nutritious upland sheep pastures under moderately high grazing intensity (evidence: presence of *Nardus stricta*, *Festuca vivipara* and *Agrostis spp.*), with patches of low grazing intensity (evidence: existence of *Calluna vulgaris*, which suggests this grassland could revert back to wet heath if left ungrazed).
B1	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Nardo-caricetum binervis* (NVC: U4(d), CG11(b), U5), *Caricetum paniceo-tumidicarpae* (NVC: M11(a)?), *Narthecio-ericetum tetralicis* (NVC: M16(d)) and *Pleurozio purpureae-ericetum tetralicis* (NVC: M17(a))	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11) and Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6)	U5: *Nardus stricta-Galium saxatile* grassland, M15: *Scirpus cespitosus-Erica tetralix* wet heath, M25: *Molinia caerulea-Potentilla erecta* mire and H4: *Ulex gallii-Agrostis curtisii* heath	Mosaic of lowland and upland grassland, wet heath and blanket bog. Maintained by grazing. *Nardus stricta-Galium saxatile* grassland widespread on uplands primarily grazed by breeding ewes. Grazing pressure appears to be intermediate as there is a high cover of *Calluna vulgaris* and *Molinia caerulea* but also much *Nardus stricta*, *Juncus squarrosus* and *Agrostis spp*. This may also be an indication of previous drainage of the land.
B2	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Nardo-Caricetum binervis* (NVC: U4(d), CG11(b), U5), *Hylocomio-Centaureetum nigrae* (NVC: U4(d), CG11(b), CG10(a)), *Narthecio-ericetum tetralicis* (NVC: M16(d)), *Carici nigrae-juncetum articulati* (NVC: M5, M6, M7, M8) and *Pleurozio purpureae-ericetum tetralicis* (NVC: M17(a))	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11) and Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6)	U5: *Nardus stricta-Galium saxatile* grassland, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, M25: *Molinia caerulea-Potentilla erecta* mire, H4: *Ulex gallii-Agrostis curtisii* heath and MG5: *Cynosurus cristatus-Centaurea nigra* grassland	Mosaic of lowland and nutritious upland grassland, wet heath and blanket bog. Maintained by grazing. *Nardus stricta-Galium saxatile* grassland widespread on uplands primarily grazed by breeding ewes. Grazing pressure appears to be greater than B1 as there is a high cover of *Nardus stricta*, *Juncus spp.* and *Agrostis spp*. *Festuca vivipara* is also present and *Molinia caerulea* appears to dominate at the expense of dwarf shrubs.
B3	Associations: *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Nardo-Caricetum binervis* (NVC: U4(d), CG11(b), U5) and *Hylocomio-Centaureetum nigrae* (NVC: U4(d), CG11(b), CG10(a))	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11) and Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6)	U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, H4: *Ulex gallii-Agrostis curtisii* heath, U5: *Nardus stricta-Galium saxatile* grassland, M25: *Molinia caerulea-Potentilla erecta* mire and MG5: *Cynosurus cristatus-Centaurea nigra* grassland	Mosaic of lowland and nutritious upland grassland, wet heath and blanket bog. Maintained by grazing. *Nardus stricta-Galium saxatile* grassland widespread on uplands primarily grazed by breeding ewes. A relatively high level of grazing suggested by dominance of *Festuca vivipara*, *Agrostis spp.* and *Potentilla erecta*. However presence of *Ulex gallii* indicates ungrazed patches.

B4	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Associations: *Senecioni-juncetum acutiflori* (NVC: M22(b), M22, M24(b)), *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)) and *Narthecio-ericetum tetralicis* (NVC: M16(d))	Dry calcareous & neutral grassland (Order: *Arrhenatheretalia* (*Cynosurion cristati*, NVC: MG4, MG5, MG6), Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11), Improved agricultural grassland (Order: *Polygono arenastri-Poetalia annuae*, NVC: MG7) and Wet grassland (Order: *Molinietalia caeruleae* (*Junco conglomerati-Molinion*, NVC: M24, M25 and *Juncion acutiflori*, NVC: M23)	U5: *Nardus stricta-Galium saxatile* grassland, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, MG10: *Holcus lanatus-Juncus effusus* rush-pasture and M23: *Juncus effusus /acutiflorus-Galium palustre* rush-pasture	Mosaic of damp lowland and nutritious upland grassland. Maintained by grazing. *Nardus stricta-Galium saxatile* grassland widespread on uplands primarily grazed by breeding ewes. A moderate level of grazing suggested by dominance of *Molinia caerulea*, *Agrostis spp.*, *Juncus spp.* and *Poa spp.* However presence of *Ulex gallii* and dwarf shrub species indicates ungrazed patches.
B5	Class: *Molinio-Arrhenatheretea* (NVC: M22-M28, MG1-MG6, MG8-MG10), Associations: *Senecioni-juncetum acutiflori* (NVC: M22(b), M22, M24(b)), *Achilleo-Festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)) and *Nardo-Caricetum binervis* (NVC: U4(d), CG11(b), U5)	Dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11)	U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland, U5: *Nardus stricta-Galium saxatile* grassland and MG10: *Holcus lanatus-Juncus effusus* rush-pasture	Mosaic of damp lowland and nutritious upland grassland. Maintained by grazing. *Nardus stricta-Galium saxatile* grassland widespread on uplands primarily grazed by breeding ewes. High grazing level likely due to dominant cover of *Nardus stricta*, *Juncus spp.*, *Agrostis spp.*, *Festuca vivipara*, *Galium saxatile* and presence of *Lolium perenne*. However the presence of *Holcus lanatus*, *Festuca rubra*, *Vaccinium myrtillus* and *Erica spp.* also suggest patches of ungrazed land.
C1	Class: *Oxycocco-sphagnetea* (NVC: M14-M21, H5), Orders: *Sphagnetalia compacti* (NVC: M16), *Vaccinio-genistetalia* (NVC: H1-H4, H6-H12, H16, H21), Alliance: *Vaccinio-callunion* (NVC: H1, H9), Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Narthecio-ericetum tetralicis* (NVC: M16(d)), *Vaccinio-ericetum tetralicis* (NVC: M19(a)), Alliance: *Nardo-galion saxatilis* (NVC: CG10, CG11), Association: *Hylocomio-centaureatum nigrae* (NVC: U4(d), CG11(b), CG10(a))	Mosaic of upland blanket bog, lowland blanket bog, raised bog (Class: *Oxycocco-sphagnetea*, Order: *Sphagnetalia magellanici*, NVC: M17-M21) and wet heath (Order: *Erico-sphagnetalia papillosi*, NVC: M14-M16, H5)	M15: *Scirpus cespitosus-Erica tetralix* wet heath	Mosaic of upland Atlantic blanket bog and wet heath, as characterised by species such as *Andromeda polifolia*. Wet heath may develop from blanket bog in response to grazing. Grazing is necessary in this habitat to reduce competition from *Calluna vulgaris*, however too much grazing would result in a species-poor sward of *Trichophorum caespitosum*. Equal coverage of *Calluna* and *Trichophorum*, however, suggests a moderate grazing level, although the higher cover of *Empetrum nigrum* and *Eriophorum angustifolium* may indicate a higher level of grazing.

C2	Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Narthecio-ericetum tetralicis* (NVC: M16(d)), *Lycopodio-rhynchosporetum albo-fuscae* (NVC: M16(c)), *Pleurozio purpureae-ericetum tetralicis* (NVC: M17(a)), Order: *Nardetalia* (NVC: U2, U3, U4, U5, U6, CG10, CG11), Alliance: *Nardo-galion saxatilis* (NVC: CG10, CG11)	Mosaic of Lowland blanket bog, raised bog (Class: *Oxycocco-sphagnetea*, Order: *Sphagnetalia magellanici*, NVC: M17-M21) and rich fen and flush (Class: *Scheuchzerio-carcetea nigrae*, Order: *Caricetalia davallianae*, NVC: M9-M13, SD13-SD15)	M15: *Scirpus cespitosus-Erica tetralix* wet heath and M16: *Erica tetralix-Sphagnum compactum* wet heath	Mosaic of upland Atlantic blanket bog and wet heath. Wet heath may develop from blanket bog in response to grazing. Grazing is necessary in this habitat to reduce competition from *Calluna vulgaris* and *Molinia caerulea*, however too much grazing would result in a species-poor sward of *Trichophorum caespitosum*. Equal coverage of *Calluna*, *Molinia* and *Trichophorum*, however, suggests a moderate to low grazing level. However there is also evidence of heavy grazing, as indicated by the presence of *Nardus stricta-Galium saxatile* and *Juncus squarrosus-Festuca ovina* grasslands, characterised by grasses such as *Nardus stricta* and *Festuca spp*. and rushes such as *Juncus spp*.
C3	Order: *Nardetalia* (NVC: U2, U3, U4, U5, U6, CG10, CG11), Alliance: *Nardo-galion saxatilis* (NVC: CG10, CG11), Associations: *Achilleo-festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Hylocomio-centaureatum nigrae* (NVC: U4(d), CG11(b), CG10(a)), Class: *Oxycocco-sphagnetea* (NVC: M14-M21, H5), Order: *Sphagnetalia compacti* (NVC: M16), Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Narthecio-ericetum tetralicis* (NVC: M16(d)), *Erico-sphagnetum magellanici* (NVC: M1, M3, M18, M20(a)), *Pleurozio purpureae-ericetum tetralicis* (NVC: M17(a)), *Vaccinio-ericetum tetralicis* (NVC: M19(a)), Order: *Molinietalia* (NVC: M26), Alliance: *Junco conglomerati-molinion* (NVC: M24, M25)	Mosaic of Lowland blanket bog, raised bog (Class: *Oxycocco-sphagnetea*, Order: *Sphagnetalia magellanici*, NVC: M17-M21), rich fen and flush (Class: *Scheuchzerio-carcetea nigrae*, Order: *Caricetalia davallianae*, NVC: M9-M13, SD13-SD15), poor fen and flush (Order: *Caricetalia nigrae*, NVC: M5-M8) and dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21)	M15: *Scirpus cespitosus-Erica tetralix* wet heath, with M17: *Scirpus cespitosus-Eriophorum vaginatum* blanket mire, M16: *Erica tetralix-Sphagnum compactum* wet heath	Broad mosaic of upland acid grass and heathland abutting *Ulex* communities, with some lowland Atlantic blanket bog. The high cover of *Erica tetralix* suggests a low level of grazing, however, there is also evidence of heavy grazing, as indicated by the presence of *Nardus stricta-Galium saxatile* and *Juncus squarrosus-Festuca ovina* grasslands, characterised by grasses such as *Nardus stricta* and *Festuca spp*. and rushes such as *Juncus spp*., as well as forbs such as *Galium saxatile*. This 'blanket bog' group is, in general, drier than the previous two groups.
C4	Order: *Nardetalia* (NVC: U2, U3, U4, U5, U6, CG10, CG11), Alliance: *Nardo-galion saxatilis* (NVC: CG10, CG11), Associations: *Achilleo-festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Hylocomio-centaureatum nigrae* (NVC: U4(d), CG11(b), CG10(a)), Order: *Sphagnetalia compacti* (NVC: M16), Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Narthecio-ericetum tetralicis* (NVC: M16(d)), *Erico-sphagnetum magellanici* (NVC: M1, M3, M18, M20(a))	Mosaic of Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21), poor fen and flush (Class: *Scheuchzerio-carcetea nigrae*, Order: *Caricetalia nigrae*, NVC: M5-M8) and lowland blanket bog (Class: *Oxycocco-sphagnetea*, Order: *Sphagnetalia magellanici*, NVC: M17-M21)	M15: *Scirpus cespitosus-Erica tetralix* wet heath, with U1: *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	Mosaic of wet heath, Atlantic blanket bog and acid grassland. The substantial cover of *Nardus stricta* and *Juncus squarrosus* indicates a high level of grazing and the most heavily grazed 'blanket bog' group. The presence of *Carex distans* in all quadrats suggests a coastal group.

C5	Order: *Nardetalia* (NVC: U2, U3, U4, U5, U6, CG10, CG11), Alliance: *Nardo-galion saxatilis* (NVC: CG10, CG11), Associations: *Nardo-caricetum binervis* (NVC: U4(d), CG11(b), U5), *Hylocomio-centaureatum nigrae* (NVC: U4(d), CG11(b), CG10(a)), Order: *Sphagnetalia compacti* (NVC: M16), Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Narthecio-ericetum tetralicis* (NVC: M16(d)),	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21)	M15: *Scirpus cespitosus-Erica tetralix* wet heath, and M16: *Erica tetralix-Sphagnum compactum* wet heath, with U1: *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	Mosaic of acid grassland and wet heath on lower mountain slopes. Again a high cover of *Nardus stricta* suggests a high level of grazing, which is supported by the presence of *Agrostis* and *Festuca* grass species, which increase as sheep numbers, and therefore the deposition of dung and urine, increase.
D1	Association: *Achilleo-festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), Order: *Quercetalia robori-petraeae* (NVC: W11, W16, W17, U20)	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21) and dense bracken (Class: *Rhamno-prunetea*, Order: *Prunetalia spinosae*, NVC: W21-W25, SD16, SD18)	U20 (a): *Pteridium aquilinum-Rubus fruticosus* community	Good quality upland sheep pasture which has been invaded by *Pteridium aquilinum*, suggesting a very low level of grazing. This community is particularly species-poor.
D2	Order: *Vaccinio-genistetalia* (NVC: H1-H4, H6-H12, H16, H21), Alliances: *Genisto-callunion* (NVC: H1, H9), *Vaccinio-callunion* (NVC: H1, H9), *Quercion robori-petaeae* (NVC: W11, W16, W17, U20), Association: *Blechno-quercetum petraeae* (NVC: W11, W16, W17)	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21) and dense bracken (Class: *Rhamno-prunetea*, Order: *Prunetalia spinosae*, NVC: W21-W25, SD16, SD18)	H10: *Calluna vulgaris-Erica cinerea* heath, H20: *Vaccinium myrtillus-Racomitrium lanuginosum* heath	Mosaic of dry *Calluna*-dominated upland heath and acid grassland. The high cover of *Pteridium aquilinum*, *Galium saxatile*, *Festuca ovina* and other grass species indicates a high level of grazing on grassland and a low grazing level on the heath.
D3	Associations: *Carici nigrae-juncetum articulati* (NVC: M5, M6, M7, M8), *Anagallido-caricetum diandrae* (NVC: M9(b)), Order: *Molinietalia* (NVC: M26), Order: *Nardetalia* (NVC: U2, U3, U4, U5, U6, CG10, CG11), Alliance: *Nardo-galion saxatilis* (NVC: CG10, CG11), Associations: *Achilleo-festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Nardo-caricetum binervis* (NVC: U4(d), CG11(b), U5), *Hylocomio-centaureatum nigrae* (NVC: U4(d), CG11(b), CG10(a)), Order: *Sphagnetalia compacti* (NVC: M16), Alliance: *Ericion tetralicis* (NVC: M14, M15, M16, H5), Associations: *Narthecio-ericetum tetralicis* (NVC: M16(d)), *Vaccinio-ericetum tetralicis* (NVC: M19(a)), Class: *Calluno-ulicetea* (NVC: U2-U6, CG10, CG11, H1-H4, H6-H12, H16, H21), Alliance: *Ulici-ericion cinereae* (NVC: H2, H8), Order: *Vaccinio-genistetalia* (NVC: H1-H4, H6-H12, H16, H21), Alliances: *Genisto-callunion* (NVC: H1, H9), *Vaccinio-callunion* (NVC: H1, H9), Association: *Blechno-quercetum petraeae* (NVC: W11, W16, W17)	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21) and dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11)	A wide mosaic of H8: *Calluna vulgaris-Ulex gallii* heath, H10: *Calluna vulgaris-Erica cinerea* heath, H21: *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath, M15: *Scirpus cespitosus-Erica tetralix* wet heath, M23: *Juncus effusus/acutiflorus-Galium palustre* rush-pasture, U4: *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland	Broad mosaic of upland wet and dry heath, grassy and shrub heathland and blanket bog. Grazing needs to be sufficiently heavy to keep scrub in check, although some patches of gorse are beneficial as shelter for livestock in bad weather. As with the plant communities, there is also a wide range of grazing states in this group. The presence of *Nardus stricta*, *Agrostis* and *Festuca spp.* and *Juncus spp.* indicates a high level of grazing and *Pteridium aquilinum* demonstrates a sheep-only system. Whereas relatively high cover of *Calluna vulgaris*, *Erica spp.*, *Molinia caerulea* and *Ulex gallii* specifies a much lower level of grazing.

D4	Association: *Vaccinio-ericetum tetralicis* (NVC: M19(a)), Class: *Calluno-ulicetea* (NVC: U2-U6, CG10, CG11, H1-H4, H6-H12, H16, H21), Order: *Vaccinio-genistetalia* (NVC: H1-H4, H6-H12, H16, H21), Alliances: *Genisto-callunion* (NVC: H1, H9), *Vaccinio-callunion* (NVC: H1, H9), Association: *Blechno-quercetum petraeae* (NVC: W11, W16, W17)	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21) and dry-humid acid grassland (Order: *Nardetalia strictae*, NVC: U2, U3, U4, U5, CG10, CG11)	H10: *Calluna vulgaris-Erica cinerea* heath	Mosaic of dry upland heath and acid grassland. The presence of the *Blechno-quercetum petraeae* association suggests that this community is ungrazed or very lightly grazed. This is supported by a high cover of *Calluna vulgaris*, *Vaccinium myrtillus* and *Cladonia spp.*, although perhaps there was some grazing in the past as there is a large percentage of *Festuca ovina* and *Agrostis spp*.
D5	Order: *Vaccinio-genistetalia* (NVC: H1-H4, H6-H12, H16, H21), Alliance: *Genisto-callunion* (NVC: H1, H9), Association: *Hyperico-dryadetum* (NVC: CG13?), Alliance: *Vaccinio-callunion* (NVC: H1, H9), Associations: *Lycopodio alpini-rhacomitrietum lanuginosi* (NVC: H15), *Herberteto-polytrichetum alpini* (NVC: H21), *Achilleo-festucetum tenuifoliae* (NVC: MG5, U4(d), CG11(b), CG10(a)), *Nardo-caricetum binervis* (NVC: U4(d), CG11(b), U5)	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21), wet heath (Class: *Oxycocco-sphagnetea*, Order: *Erico-sphagnetalia papillosi*, NVC: M14-M16, H5) and montane heath (Class: *Carici rupestris-kobresietea bellardii*, Order: *Kobresio-dryadetalia*, NVC: CG12, CG13, CG14) and (Class: *Loiseleurio-vaccinietea*, Order: *Rhododendro-vaccinietalia*, NVC: H13-H15, H17-H20, H22)	U5: *Nardus stricta-Galium saxatile* grassland and H10: *Calluna vulgaris-Erica cinerea* heath	Mosaic of wind-clipped dwarf shrub heath of mountain summits and dry grassy upland heath of steep sheltered slopes. There was a substantial bryophyte layer, suggesting a low level of sheep grazing, with perhaps some grazing by hare and grouse. The high cover of mosses *Racomitrium lanuginosum* and *Pleurozium schreberi* are characteristic of montane heath.
E1	Order: *Molinietalia* (NVC: M26), Alliance: *Junco conglomerati-molinion* (NVC: M24, M25), Associations: *Myricetum gale* (NVC: M25), *Osmundo-salicetum atrocinereae* (NVC: W2, W3), Alliance: *Dicrano-pinion* (NVC: W18, W19)	Mosaic of Bog woodland (Class: *Vaccinio-piceetea*, Order: *Piceetalia excelsae*, NVC: W4, W18, W19), scrub (Class: *Rhamno-prunetea*, Order: *Prunetalia spinosae*, NVC: W21-W25, SD16, SD18), wet willow-alder-ash woodland (Class: *Alnetea glutinosae*, Order: *Salicetalia auritae*, NVC: W2, W3), Order: *Alnetalia glutinosae*, NVC: W1, W5), wet pedunculate oak-ash woodland (Class: *Querco-fagetea*, Order: *Fagetalia-sylvaticae*, NVC: W7-W10, W12-W15), dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21) and poor fen and flush (Class: *Scheuchzerio-carcetea nigrae*, Order: *Caricetalia nigrae*, NVC: M5-M8)	W23: *Ulex europaeus-Rubus fruticosus* scrub, W24: *Rubus fruticosus-Holcus lanatus* underscrub, W25: *Pteridium aquilinum-Rubus fruticosus* underscrub, W21: *Crataegus monogyna-Hedera helix* scrub, W6: *Alnus glutinosa-Urtica dioica* woodland, W4: *Betula pubescens-Molinia caerulea* woodland	Mosaic of bog woodland, other deciduous woodland types and scrub. This group is subject to very light grazing or no grazing, perhaps due to the wet conditions. However a high cover of *Pteridium aquilinum* indicates a relatively high level of grazing in the past.
E2	Order: *Ulicetalia minoris* (NVC: H11), Alliances: *Ulici-ericion cinereae* (NVC: H2, H8), *Sarothamnion scopariae* (NVC: W23), Class: *Calluno-ulicetea* (NVC: U2-U6, CG10, CG11, H1-H4, H6-H12, H16, H21)	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21), wet heath (Class: *Oxycocco-sphagnetea*, Order: *Erico-sphagnetalia papillosi*, NVC: M14-M16, H5), rich fen and flush (Class: *Scheuchzerio-carcetea nigrae*, Order: *Caricetalia davallianae*, NVC: M9-M13, SD13-SD15) and scrub (Class: *Rhamno-prunetea*, Order: *Prunetalia spinosae*, NVC: W21-W25, SD16, SD18)	W23: *Ulex europaeus-Rubus fruticosus* scrub, W18: *Pinus sylvestris-Hylocomium splendens* woodland	This ‘woodland and scrub’ group appears to be mainly ungrazed low altitude shrub-heath. It consists primarily of *Erica spp.*, *Molinia caerulea* and *Ulex europaeus*.

E3	Alliance: *Arrhenatherion elatius* (NVC: MG1), Order: *Nardetalia* (NVC: U2, U3, U4, U5, U6, CG10, CG11), Associations: *Hylocomio-centaureatum nigrae* (NVC: U4(d), CG11(b), CG10(a)), *Pleurozio purpureae-ericetum tetralicis* (NVC: M17(a)), Class: *Calluno-ulicetea* (NVC: U2-U6, CG10, CG11, H1-H4, H6-H12, H16, H21), Alliance: *Ulici-ericion cinereae* (NVC: H2, H8), Order: *Vaccinio-genistetalia* (NVC: H1-H4, H6-H12, H16, H21), Alliance: *Genisto-callunion* (NVC: H1, H9)	Dry siliceous heath (Class: *Calluno-ulicetea*, Order: *Calluno-ulicetalia*, NVC: H1-H4, H6-H12, H16, H21), wet heath (Class: *Oxycocco-sphagnetea*, Order: *Erico-sphagnetalia papillosi*, NVC: M14-M16, H5), rich fen and flush (Class: *Scheuchzerio-carcetea nigrae*, Order: *Caricetalia davallianae*, NVC: M9-M13, SD13-SD15) and scrub (Class: *Rhamno-prunetea*, Order: *Prunetalia spinosae*, NVC: W21-W25, SD16, SD18)	M25: *Molinia caerulea-Potentilla erecta* mire, H1: *Calluna vulgaris-Festuca ovina* heath, H4: *Ulex gallii-Agrostis curtisii* heath, M15: *Scirpus cespitosus-Erica tetralix* wet heath, W25: *Pteridium aquilinum-Rubus fruticosus* underscrub	Dry lowland gorse heathland. The high cover of *Calluna vulgaris*, *Erica spp.*, *Molinia caerulea* and *Ulex gallii* suggests a general lack of grazing.

S3.1 Ordination axes and corresponding significant correlations for environmental variables and carabid species.

Variable/ species	Ordination axis	Correlation	*P*
Altitude	1	$r_s = 0.249$	$p = 0.015$
	2	$r_s = 0.23$	$p = 0.025$
	3	$r_s = -0.376$	$p < 0.01$
Plant diversity	3	$r_s = 0.203$	$p = 0.049$
Plant functional diversity	1	$r_s = 0.26$	$p = 0.011$
	2	$r_s = 0.29$	$p < 0.01$
	3	$r_s = -0.679$	$p < 0.0001$
% dung	1	$r_s = 0.416$	$p < 0.0001$
% forbs	1	$r_s = -0.306$	$p < 0.01$
	3	$r_s = 0.588$	$p < 0.0001$
% rushes	1	$r_s = 0.322$	$p < 0.01$
	3	$r_s = -0.301$	$p < 0.01$
Habitat diversity	1	$r_s = -0.238$	$p = 0.02$
% Scrub	1	$r_s = -0.219$	$p = 0.03$
% Upland blanket bog	1	$r_s = 0.205$	$p = 0.047$
% Dry humid acid grassland	1	$r_s = 0.225$	$p = 0.03$
Vegetation height	1	$r_s = -0.436$	$p < 0.0001$
Soil depth	1	$r_s = 0.265$	$p < 0.01$
	3	$r_s = -0.554$	$p < 0.0001$
Soil pH	1	$r_s = -0.245$	$p = 0.02$
	2	$r_s = -0.305$	$p < 0.01$
	3	$r_s = 0.52$	$p < 0.0001$
Soil nitrogen	1	$r_s = 0.234$	$p = 0.023$
	2	$r_s = 0.274$	$p < 0.01$
	3	$r_s = -0.619$	$p < 0.0001$
Soil carbon	1	$r_s = 0.266$	$p < 0.01$
	3	$r_s = -0.377$	$p < 0.01$
Soil moisture	2	$r_s = -0.296$	$p < 0.01$
	3	$r_s = 0.551$	$p < 0.0001$
% bare ground	3	$r_s = -0.291$	$p < 0.01$
% litter	1	$r_s = -0.317$	$p < 0.01$
	3	$r_s = -0.202$	$p = 0.049$
% signs of grazing	1	$r_s = 0.329$	$p < 0.01$
	3	$r_s = 0.319$	$p < 0.01$
% shrubs	2	$r_s = 0.308$	$p < 0.01$
	3	$r_s = -0.492$	$p < 0.0001$
% traditional ewes	2	$r_s = 0.264$	$p < 0.01$
Sheep stocking rate	1	$r_s = 0.407$	$p < 0.0001$
Abax parallelepipidus	1	$r_s = -0.684$	$p < 0.0001$
	2	$r_s = 0.229$	$p = 0.026$
Agonum fuliginosum	2	$r_s = -0.38$	$p < 0.01$
Agonum muelleri	2	$r_s = -0.251$	$p = 0.014$
	3	$r_s = 0.406$	$p < 0.0001$
Agonum thoreyi	2	$r_s = -0.301$	$p < 0.01$
Calathus fuscipes	3	$r_s = 0.407$	$p < 0.0001$
Carabus clatratus	1	$r_s = 0.371$	$p < 0.01$
	3	$r_s = -0.303$	$p < 0.01$
Carabus granulatus	1	$r_s = -0.344$	$p < 0.01$
Carabus problematicus	1	$r_s = 0.42$	$p < 0.0001$
	2	$r_s = 0.335$	$p < 0.01$
Nebria brevicollis	1	$r_s = 0.287$	$p < 0.01$
	3	$r_s = 0.638$	$p < 0.0001$
Nebria salina	1	$r_s = 0.64$	$p < 0.0001$
	2	$r_s = 0.53$	$p < 0.0001$

Poecilus versicolor	3	$r_s = 0.522$	$p < 0.0001$
Pterostichus diligens	3	$r_s = -0.47$	$p < 0.0001$
Pterostichus madidus	1	$r_s = -0.346$	$p < 0.01$
	3	$r_s = 0.577$	$p < 0.0001$
Pterostichus melanarius	1	$r_s = -0.227$	$p = 0.027$
	2	$r_s = -0.393$	$p < 0.0001$
	3	$r_s = 0.43$	$p < 0.0001$
Pterostichus niger	1	$r_s = -0.53$	$p < 0.0001$
	2	$r_s = -0.568$	$p < 0.0001$
Pterostichus nigrita	2	$r_s = -0.461$	$p < 0.0001$
Pterostichus rhaeticus	1	$r_s = 0.278$	$p < 0.01$
	3	$r_s = -0.327$	$p < 0.01$
Pterostichus strenuous	2	$r_s = -0.374$	$p < 0.01$
	3	$r_s = 0.505$	$p < 0.0001$
Pterostichus vernalis	2	$r_s = -0.314$	$p < 0.01$
	3	$r_s = 0.508$	$p < 0.0001$

S3.2 Ordination axes and corresponding significant correlations for environmental variables and generalist predator carabid species.

Variable/ species	Ordination axis	Correlation	*P*
Altitude	1	$r_s = -0.43$	$p < 0.0001$
	2	$r_s = 0.355$	$p < 0.01$
Plant functional diversity	1	$r_s = -0.718$	$p < 0.0001$
	2	$r_s = 0.362$	$p < 0.01$
% dung	3	$r_s = 0.458$	$p < 0.0001$
% forbs	1	$r_s = 0.556$	$p < 0.0001$
	2	$r_s = -0.444$	$p < 0.0001$
% rushes	1	$r_s = -0.498$	$p < 0.0001$
Habitat diversity	3	$r_s = -0.287$	$p < 0.01$
% Upland blanket bog	3	$r_s = 0.247$	$p = 0.02$
Vegetation height	3	$r_s = -0.463$	$p < 0.0001$
Soil depth	1	$r_s = -0.53$	$p < 0.0001$
	2	$r_s = 0.224$	$p = 0.029$
Soil pH	1	$r_s = 0.584$	$p < 0.0001$
	2	$r_s = -0.362$	$p < 0.01$
Soil nitrogen	1	$r_s = -0.652$	$p < 0.0001$
	2	$r_s = 0.316$	$p < 0.01$
Soil carbon	1	$r_s = -0.356$	$p < 0.01$
	2	$r_s = 0.228$	$p < 0.026$
Soil phosphorus	1	$r_s = -0.224$	$p < 0.029$
Soil moisture	1	$r_s = 0.587$	$p < 0.0001$
	2	$r_s = -0.29$	$p < 0.01$
% bare ground	1	$r_s = -0.305$	$p < 0.01$
% litter	3	$r_s = -0.439$	$p < 0.0001$
% signs of grazing	2	$r_s = -0.212$	$p < 0.04$
	3	$r_s = 0.49$	$p < 0.0001$
% shrubs	1	$r_s = -0.34$	$p < 0.01$
	2	$r_s = 0.537$	$p < 0.0001$
	3	$r_s = -0.288$	$p < 0.01$
Sheep stocking rate	3	$r_s = 0.427$	$p < 0.0001$
Abax parallelepipidus	3	$r_s = -0.659$	$p < 0.0001$
Agonum fuliginosum	1	$r_s = 0.207$	$p = 0.045$
Agonum muelleri	1	$r_s = 0.312$	$p < 0.01$
	2	$r_s = -0.342$	$p < 0.01$
Calathus fuscipes	1	$r_s = 0.27$	$p < 0.01$
	3	$r_s = 0.289$	$p < 0.01$
Carabus clatratus	1	$r_s = -0.432$	$p < 0.0001$
	3	$r_s = 0.206$	$p = 0.045$
Carabus granulatus	2	$r_s = -0.284$	$p < 0.01$
	3	$r_s = -0.284$	$p < 0.01$
Carabus problematicus	2	$r_s = 0.717$	$p < 0.0001$
	3	$r_s = 0.25$	$p = 0.015$
Nebria brevicollis	1	$r_s = 0.346$	$p < 0.01$
	3	$r_s = 0.535$	$p < 0.0001$
Nebria salina	1	$r_s = -0.348$	$p < 0.01$
	2	$r_s = 0.516$	$p < 0.0001$
	3	$r_s = 0.53$	$p < 0.0001$
Poecilus versicolor	1	$r_s = 0.446$	$p < 0.0001$
	2	$r_s = -0.27$	$p < 0.01$
	3	$r_s = 0.203$	$p = 0.048$
Pterostichus diligens	1	$r_s = -0.47$	$p < 0.0001$
	2	$r_s = -0.329$	$p < 0.01$
Pterostichus madidus	1	$r_s = 0.52$	$p < 0.0001$
	2	$r_s = -0.402$	$p < 0.0001$

Pterostichus melanarius	1	$r_s = 0.446$	$p < 0.0001$
	2	$r_s = -0.474$	$p < 0.0001$
Pterostichus niger	1	$r_s = 0.554$	$p < 0.0001$
	3	$r_s = -0.423$	$p < 0.0001$
Pterostichus nigrita	2	$r_s = -0.499$	$p < 0.0001$
	3	$r_s = 0.206$	$p = 0.046$
Pterostichus rhaeticus	1	$r_s = -0.453$	$p < 0.0001$
Pterostichus strenuous	1	$r_s = 0.442$	$p < 0.0001$
	2	$r_s = -0.413$	$p < 0.0001$
Pterostichus vernalis	1	$r_s = 0.518$	$p < 0.0001$
	2	$r_s = -0.355$	$p < 0.01$

S3.3 Ordination axes and corresponding significant correlations for environmental variables and specialist predator carabid species.

Variable/ species	Ordination axis	Correlation	P
Altitude	2	$r_s = 0.533$	$p = 0.019$
Plant biomass	1	$r_s = 0.485$	$p = 0.035$
% upland blanket bog	2	$r_s = 0.503$	$p = 0.028$
Vegetation height	2	$r_s = -0.653$	$p < 0.01$
Soil phosphorus	2	$r_s = 0.486$	$p = 0.035$
% traditional ewes	1	$r_s = 0.725$	$p < 0.01$
Cychrus carabodies	2	$r_s = -0.708$	$p < 0.01$
Notiophilus germinyi	1	$r_s = 0.744$	$p < 0.01$
Notiophilus palustris	1	$r_s = -0.597$	$p < 0.01$
Trechus obtusus	2	$r_s = 0.784$	$p < 0.0001$

S3.4 Ordination axes and corresponding significant correlations for environmental variables and phytophagous carabid species.

Variable/ species	Ordination axis	Correlation	P
Altitude	2	$r_s = -0.936$	$p < 0.01$
Plant diversity	2	$r_s = 0.771$	$p = 0.043$
% dung	3	$r_s = 0.887$	$p < 0.01$
% forbs	1	$r_s = 0.812$	$p = 0.027$
Habitat diversity	3	$r_s = -0.932$	$p < 0.01$
% scrub	2	$r_s = 0.903$	$p < 0.01$
	3	$r_s = -0.867$	$p = 0.01$
Vegetation height	3	$r_s = -0.887$	$p < 0.01$
Soil pH	1	$r_s = 0.887$	$p < 0.01$
% improved grassland	2	$r_s = 0.906$	$p < 0.01$
% lowland blanket bog	2	$r_s = 0.962$	$p < 0.01$
% signs of grazing	3	$r_s = 0.887$	$p < 0.01$
% shrubs	1	$r_s = -0.805$	$p = 0.029$
Stocking rate of sheep	2	$r_s = -0.962$	$p < 0.01$
Amara lunicollis	2	$r_s = 0.913$	$p < 0.01$
	3	$r_s = -0.877$	$p < 0.01$
Amara plebeja	1	$r_s = 0.817$	$p = 0.025$

S4.1 Pairwise comparisons between habitat types in 2007. DHAG is dry humid acid grassland and LBB is lowland blanket bog.

2007	**1**	**2**	**5**	**6**	**7**	**9**	**10**	**11**	**12**
	improved grassland (IG)	**wet grassland (WG)**	**upland blanket bog (UBB)**	**eroding blanket bog (EBB)**	**wet heath (WH)**	**dry siliceous heath (DSH)**	**scrub**	**wood edge**	**bracken**
Simpsons	estimate -0.165 ± s.e. 0.073 (DHAG) estimate -0.395 ± s.e. 0.162 (EBB) estimate -0.281 ± s.e. 0.097 (DSH)			estimate -0.381 ± s.e. 0.171 (WG) estimate -0.341 ± s.e. 0.141 (UBB)		estimate -0.228 ± s.e. 0.106 (UBB)	estimate 0.321 ± s.e. 0.110 (DHAG) estimate 0.273 ± s.e. 0.115 (LBB) estimate 0.552 ± s.e. 0.177 (EBB) estimate 0.291 ± s.e. 0.135 (WH) estimate 0.438 ± s.e. 0.117 (DSH)	estimate 0.393 ± s.e. 0.186 (DHAG) estimate 0.623 ± s.e. 0.229 (EBB) estimate 0.509 ± s.e. 0.194 (DSH)	
Richness	estimate -1.008 ± s.e. 0.47 (EBB)						estimate 1.088 ± s.e. 0.477 (WG) estimate 1.812 ± s.e. 0.650 (EBB) estimate 1.092 ± s.e. 0.318 (DSH)	estimate 0.754 ± s.e. 0.372 (WG) estimate 1.477 ± s.e. 0.543 (EBB) estimate 0.758 ± s.e. 0.342 (DSH)	
Sorensens (measure of similarity, so high similarity means low beta diversity)	estimate 0.091 ± s.e. 0.038 (WG) estimate 0.103 ± s.e. 0.042 (Scrub)	estimate -0.113 ± s.e. 0.04 (LBB) estimate -0.158 ± s.e. 0.055 (EBB) estimate -0.095 ± s.e. 0.044 (DSH)	estimate -0.132 ± s.e. 0.041 (WG) estimate -0.066 ± s.e. 0.028 (DHAG)		estimate 0.056 ± s.e. 0.026 (UBB)		estimate 0.125 ± s.e. 0.045 (LBB) estimate 0.144 ± s.e. 0.048 (UBB) estimate 0.170 ± s.e. 0.061 (EBB) estimate 0.107 ± s.e. 0.043 (DSH)		estimate 0.136 ± s.e. 0.058 (UBB) estimate 0.162 ± s.e. 0.068 (EBB)

S4.2 Pairwise comparisons between habitat types in 2008. DHAG is dry humid acid grassland and LBB is lowland blanket bog.

2008	1	9	10
	improved grassland (IG)	**dry siliceous heath (DSH)**	**scrub**
Density	estimate -0.235 ± s.e. 0.07 (DHAG) estimate -0.296 ± s.e. 0.05 (LBB) estimate -0.273 ± s.e. 0.067 (UBB) estimate -0.289 ± s.e. 0.077 (WH) estimate -0.766 ± s.e. 0.148 (DSH)	estimate -0.531 ± s.e. 0.168 (DHAG) estimate -0.470 ± s.e. 0.154 (LBB) estimate -0.492 ± s.e. 0.167 (UBB) estimate -0.476 ± s.e. 0.162 (WH)	estimate 0.221 ± s.e. 0.092 (DHAG) estimate 0.282 ± s.e. 0.082 (LBB) estimate 0.259 ± s.e. 0.086 (UBB) estimate 0.275 ± s.e. 0.094 (WH) estimate 0.751 ± s.e. 0.165 (DSH)
Simpsons	estimate -0.195 ± s.e. 0.061 (DHAG) estimate -0.23 ± s.e. 0.045 (LBB) estimate -0.22 ± s.e. 0.058 (UBB) estimate -0.28 ± s.e. 0.066 (WH) estimate -0.60 ± s.e. 0.128 (DSH)	estimate -0.409 ± s.e. 0.145 (DHAG) estimate -0.373 ± s.e. 0.133 (LBB) estimate -0.383 ± s.e. 0.144 (UBB) estimate -0.322 ± s.e. 0.140 (WH)	estimate 0.161 ± s.e. 0.079 (DHAG) estimate 0.196 ± s.e. 0.070 (LBB) estimate 0.186 ± s.e. 0.074 (UBB) estimate 0.247 ± s.e. 0.081 (WH) estimate 0.570 ± s.e. 0.142 (DSH)
Richness	estimate -0.419 ± s.e. 0.152 (DHAG) estimate -0.377 ± s.e. 0.095 (LBB) estimate -0.483 ± s.e. 0.145 (UBB) estimate -0.674 ± s.e. 0.181 (WH) estimate -1.238 ± s.e. 0.393 (DSH)	estimate -0.861 ± s.e. 0.401 (LBB)	estimate 0.393 ± s.e. 0.183 (DHAG) estimate 0.352 ± s.e. 0.145 (LBB) estimate 0.458 ± s.e. 0.171 (UBB) estimate 0.649 ± s.e. 0.201 (WH) estimate 1.212 ± s.e. 0.413 (DSH)

S5.1 Individual bird species significant correlations for all data in 2007: Axis 1 (altitude, soil and plant variables) and Axis 2 (habitat type, habitat diversity and grazing management).

Year	Data set	Bird species	Ordination axis	Correlation	P
2007	All	Blackbird	1	-0.701	<0.0001
			2	-0.37	<0.0001
		Blue tit	1	-0.483	<0.0001
		Chaffinch	1	-0.736	<0.0001
			2	-0.202	0.027
		Coal Tit	1	-0.245	0.007
		Dunnock	1	-0.315	<0.0001
		Goldfinch	1	-0.235	0.01
		Great Tit	1	-0.423	<0.0001
			2	-0.184	0.045
		Greenfinch	1	-0.358	<0.0001
		Hooded Crow	1	-0.354	<0.0001
			2	-0.305	0.001
		House Sparrow	1	-0.319	<0.0001
			2	-0.305	0.001
		Jackdaw	1	-0.429	<0.0001
			2	-0.219	0.017
		Linnet	1	-0.382	<0.0001
		Magpie	1	-0.477	<0.0001
			2	-0.317	<0.0001
		Meadow Pipit	1	0.67	<0.0001
			2	0.26	0.004
		Pheasant	1	-0.243	0.008
		Pied Wagtail	1	-0.285	0.002
			2	-0.358	<0.0001
		Raven	2	0.205	0.025
		Lesser Redpoll	2	0.198	0.031
		Robin	1	-0.75	<0.0001
			2	-0.333	<0.0001
		Skylark	1	0.431	<0.0001
		Song Thrush	1	-0.471	<0.0001
		Starling	1	-0.492	<0.0001
			2	-0.484	<0.0001
		Stonechat	2	0.308	0.001
		Swallow	1	-0.648	<0.0001
			2	-0.479	<0.0001
		Wheatear	1	0.258	0.005
		Willow Warbler	1	-0.379	<0.0001
		Wood Pigeon	1	-0.432	<0.0001
			2	-0.228	0.013
		Wren	1	-0.57	<0.0001
			2	0.383	<0.0001

S5.2 Individual bird species significant correlations for lowland data in 2007: Axis 1 (habitat diversity and grazing management), Axis 2 (shrub cover) and Axis 3 (soil and plant variables).

Year	Data set	Bird species	Ordination axis	Correlation	P
2007	Lowlands	Blackbird	3	-0.694	<0.0001
		Blue tit	1	-0.341	0.004
			3	-0.465	<0.0001
		Chaffinch	2	-0.4	0.001
			3	-0.573	<0.0001
		Cuckoo	1	0.243	0.046
		Goldfinch	3	-0.352	0.003
		Great Tit	3	-0.494	<0.0001
		Greenfinch	3	-0.394	0.001
		House Sparrow	3	-0.425	<0.0001
		Jackdaw	2	-0.319	0.008
			3	-0.434	<0.001
		Linnet	3	-0.296	0.014
		Magpie	3	-0.515	<0.0001
		Meadow Pipit	2	0.449	<0.0001
			3	0.659	<0.0001
		Pied Wagtail	1	0.362	0.002
		Lesser Redpoll	1	-0.248	0.041
		Robin	2	-0.306	0.011
			3	-0.735	<0.0001
		Skylark	3	0.613	<0.0001
		Snipe	1	0.24	0.048
			2	0.317	0.008
		Song Thrush	3	-0.415	<0.0001
		Starling	1	0.284	0.019
			2	-0.544	<0.0001
			3	-0.466	<0.0001
		Stonechat	1	-0.406	0.001
			3	0.306	0.011
		Swallow	1	0.369	0.002
			3	-0.662	<0.0001
		Willow Warbler	2	0.465	<0.0001
		Wood Pigeon	2	-0.267	0.028
			3	-0.394	0.001
		Wren	1	-0.697	<0.0001
			2	0.309	0.01
			3	-0.247	0.042

S5.3 Individual bird species significant correlations for upland data in 2007: Axis 1 (altitude, soil and plant variables) and Axis 2 (grazing management).

Year	Data set	Bird species	Ordination axis	Correlation	P
2007	Uplands	Blackbird	1	-0.332	0.017
		Dunnock	1	-0.344	0.013
			2	0.319	0.023
		Magpie	1	-0.309	0.027
		Meadow Pipit	1	0.407	0.003
			2	0.733	<0.0001
		Lesser Redpoll	1	-0.317	0.023
		Skylark	2	-0.336	0.016
		Stonechat	1	-0.385	0.005
		Swallow	1	-0.337	0.016
			2	0.282	0.045
		Wren	1	-0.771	<0.0001
			2	0.556	<0.0001

S5.4 Individual bird species significant correlations for all data in 2008: Axis 1 (altitude and habitat variables) and Axis 2 (?).

Year	Data set	Bird species	Ordination axis	Correlation	P
2008	All	Blackbird	1	-0.656	<0.0001
			2	0.27	0.003
		Blue tit	1	-0.63	<0.0001
			2	0.291	0.001
		Bullfinch	1	-0.205	0.025
		Chaffinch	1	-0.701	<0.0001
			2	0.214	0.02
		Chiff-Chaff	1	-0.211	0.021
		Chough	2	0.193	0.036
		Coal Tit	1	-0.425	<0.0001
		Common Sandpiper	2	-0.183	0.047
		Dunnock	1	-0.563	<0.0001
		Goldcrest	1	-0.295	0.001
		Great Tit	1	-0.564	<0.0001
			2	0.261	0.004
		Greenfinch	1	-0.254	0.005
		Hooded Crow	1	-0.523	<0.0001
			2	0.244	0.008
		Jackdaw	1	-0.466	<0.0001
			2	0.289	0.001
		Magpie	1	-0.519	<0.0001
			2	0.326	<0.0001
		Meadow Pipit	1	0.409	<0.0001
			2	-0.597	<0.0001
		Mistle Thrush	1	-0.336	<0.0001
		Pied Wagtail	1	-0.389	<0.0001
		Robin	1	-0.776	<0.0001
			2	0.401	<0.0001
		Sedge Warbler	1	-0.255	0.005
		Skylark	1	0.304	0.001
			2	-0.378	<0.0001
		Song Thrush	1	-0.623	<0.0001
			2	0.195	0.033
		Starling	1	-0.443	<0.0001
			2	0.346	<0.0001
		Swallow	1	-0.62	<0.0001
		Wheatear	1	0.311	0.001
			2	-0.406	<0.0001
		Willow Warbler	1	-0.486	<0.0001
		Wood Pigeon	1	-0.498	<0.0001
		Wren	1	-0.553	<0.0001
			2	0.42	<0.0001

S5.5 Individual bird species significant correlations for lowland data in 2008: Axis 1 (habitat diversity and grazing management) and Axis 2 (?).

Year	Data set	Bird species	Ordination axis	Correlation	P
2008	Lowlands	Blackbird	1	0.616	<0.0001
		Blue tit	1	0.714	<0.0001
			2	0.424	0.001
		Chaffinch	1	0.695	<0.0001
			2	0.573	<0.0001
		Coal Tit	1	0.35	0.009
			2	0.297	0.029
		Goldcrest	1	0.35	0.009
		Great Tit	1	0.493	<0.0001
			2	0.611	<0.0001
		Greenfinch	1	0.294	0.031
		Hooded Crow	1	0.448	0.001
		Jackdaw	1	0.573	<0.0001
			2	0.407	0.002
		Magpie	1	0.545	<0.0001
		Meadow Pipit	1	-0.814	<0.0001
		Mistle Thrush	1	0.281	0.039
		Pied Wagtail	1	0.341	0.012
			2	0.377	0.005
		Robin	1	0.606	<0.0001
			2	0.285	0.037
		Skylark	1	-0.423	0.001
			2	-0.348	0.01
		Snipe	1	-0.293	0.031
		Song Thrush	1	0.478	<0.0001
			2	0.708	<0.0001
		Starling	1	0.447	0.001
			2	0.443	0.001
		Stonechat	2	-0.276	0.043
		Swallow	1	0.646	<0.0001
		Wheatear	1	-0.355	0.008
		Willow Warbler	1	0.392	0.003
		Wood Pigeon	1	0.503	<0.0001
			2	0.353	0.009
		Wren	1	0.321	0.018

S5.6 Individual bird species significant correlations for upland data in 2008: Axis 1 (grazing state) and Axis 2 (habitat evenness).

Year	Data set	Bird species	Ordination axis	Correlation	P
2008	Uplands	Chough	2	0.311	0.007
		Dunnock	1	-0.506	<0.0001
		Meadow Pipit	1	-0.396	0.001
			2	-0.683	<0.0001
		Mistle Thrush	1	-0.246	0.048
			2	-0.266	0.032
		Pheasant	2	-0.397	0.001
		Robin	1	-0.426	<0.0001
			2	0.273	0.028
		Skylark	2	-0.583	<0.0001
		Stonechat	1	-0.425	<0.0001
		Wheatear	2	-0.613	<0.0001
		Wren	1	-0.768	<0.0001
			2	0.465	<0.0001

S6.1 Results of SIMPER analysis showing the most important plant species responsible for similarity within and dissimilarity between grazing states.

	light			light-moderate			heavy		
light	Average **similarity** 26.26%								
		contrib. %	cum. %						
	Molina caerulea	29.13	29.13						
	Potentilla erecta	15.93	45.09						
	Calluna vulgaris	8.08	53.17						
	Erica tetralix	5.21	58.38						
light-moderate	Average dissimilarity 73.02%			Average **similarity** 35.54%					
		contrib. %	cum. %		contrib. %	cum. %			
	Molina caerulea	5.97	5.97	*Calluna vulgaris*	25.59	25.59			
	Calluna vulgaris	5.73	11.70	*Potentilla erecta*	12.78	38.37			
	Agrostis stolonifera	4.63	16.34	*Agrostis stolonifera*	8.31	46.68			
	Potentilla erecta	4.55	20.88	*Molina caerulea*	4.06	50.74			
heavy	Average dissimilarity 82.80%			Average dissimilarity 76.46%			Average **similarity** 30.39%		
		contrib. %	cum. %		contrib. %	cum. %		contrib. %	cum. %
	Molina caerulea	6.93	6.93	*Calluna vulgaris*	6.99	6.99	*Nardus stricta*	13.36	13.36
	Agrostis stolonifera	4.17	11.10	*Nardus stricta*	6.74	13.73	*Potentilla erecta*	7.97	21.33
	Agrostis canina	4.11	15.21	*Agrostis stolonifera*	4.58	18.32	*Agrostis stolonifera*	7.13	28.46
	Nardus stricta	4.09	19.30	*Potentilla erecta*	4.22	22.53	*Agrostis canina*	6.58	35.05

S6.2 Results of SIMPER analysis showing the most important plant species responsible for similarity within and dissimilarity between altitudinal categories

< 100m

< 100m

Average **similarity** 28.33%

	contrib. %	cum. %
Agrostis stolonifera	17.57	17.57
Holcus lanatus	12.34	29.91
Agrostis canina	11.42	41.33
Molina caerulea	10.13	51.47

100-200m

100-200m

Average dissimilarity 81.37%

	contrib. %	cum. %
Molina caerulea	6.15	6.15
Holcus lanatus	5.41	11.55
Agrostis canina	5.28	16.83
Agrostis stolonifera	4.77	21.61

Average **similarity** 23.72%

	contrib. %	cum. %
Molina caerulea	24.47	24.47
Potentilla erecta	14.86	39.33
Calluna vulgaris	7.26	46.59
Agrostis canina	4.70	51.29

200-300m

200-300m

Average dissimilarity 80.34%

	contrib. %	cum. %
Holcus lanatus	5.34	5.34
Agrostis stolonifera	5.13	10.47
Molina caerulea	4.80	15.27
Potentilla erecta	4.30	19.57

Average dissimilarity 75.38%

	contrib. %	cum. %
Molina caerulea	5.45	5.45
Trich. caespitosum	4.49	9.94
Agrostis stolonifera	4.37	14.32
Potentilla erecta	4.20	18.52

Average **similarity** 39.85%

	contrib. %	cum. %
Molina caerulea	16.42	16.42
Potentilla erecta	12.52	28.94
Calluna vulgaris	9.99	38.93
Trich. caespitosum	8.48	47.41

300-400m

300-400m

Average dissimilarity 80.47%

	contrib. %	cum. %
Calluna vulgaris	6.51	6.51
Holcus lanatus	5.50	12.01
Nardus stricta	4.79	16.80
Agrostis stolonifera	4.77	21.57

Average dissimilarity 79.43%

	contrib. %	cum. %
Pteridium aquilinum	7.06	7.06
Nardus stricta	5.80	12.86
Molina caerulea	5.32	18.18
Festuca ovina	4.83	23.00

Average dissimilarity 67.09%

	contrib. %	cum. %
Nardus stricta	5.70	5.70
Trich. caespitosum	5.07	10.78
Molina caerulea	4.74	15.52
Carex panicea	4.70	20.22

Average **similarity** 38.36%

	contrib. %	cum. %
Calluna vulgaris	24.55	24.55
Potentilla erecta	15.38	39.93
Nardus stricta	10.80	50.73
Erica tetralix	5.59	56.32

> 400m

> 400m

Average dissimilarity 85.17%

	contrib. %	cum. %
Calluna vulgaris	8.16	8.16
Holcus lanatus	4.79	12.95
Molina caerulea	4.10	17.05
Agrostis stolonifera	4.07	21.12

Average dissimilarity 78.02%

	contrib. %	cum. %
Calluna vulgaris	8.97	8.97
Sphagnum spp.	7.78	16.75
Juncus squarrosus	6.79	23.54
Trich. caespitosum	6.30	29.84

Average dissimilarity 74.98%

	contrib. %	cum. %
Calluna vulgaris	6.51	6.51
Trich. caespitosum	5.15	11.66
Molina caerulea	4.73	16.39
Potentilla erecta	4.53	20.92

Average dissimilarity 73.08%

	contrib. %	cum. %
Calluna vulgaris	6.42	6.42
Trich. caespitosum	5.86	12.28
Potentilla erecta	4.90	17.18
Vaccinium myrtillus	4.69	21.87

Average **similarity** 36.96%

	contrib. %	cum. %
Calluna vulgaris	30.63	30.63
Vaccinium myrtillus	9.29	39.92
Potentilla erecta	7.67	47.59
Juncus squarrosus	5.28	52.87

S6.3 Results of SIMPER analysis showing the most important ground beetle species responsible for similarity within and dissimilarity between grazing states. Black writing = trap scale, red writing = habitat scale.

light

light

Average **similarity** 12.55% 27.86%

	contrib. %	cum. %
Abax parallelepipidus	57.90	57.90
	42.84	42.84
Pterostichus niger	20.43	78.33
	20.52	63.36
Pterostichus madidus	5.98	84.31
Carabus granulatus	5.68	69.05
Carabus problematicus	3.36	87.67
Pterostichus nigrita	5.35	74.40

light-moderate

light-moderate

Average dissimilarity 88.31% 71.09%

	contrib. %	cum. %
Abax parallelepipidus	19.91	19.91
	14.18	14.18
Pterostichus niger	14.01	33.92
	11.56	25.74
Carabus problematicus	12.66	46.58
	11.20	36.94
Nebria brevicollis	7.41	53.99
Nebria salina	6.72	43.66

Average **similarity** 13.94% 31.19%

	contrib. %	cum. %
Abax parallelepipidus	19.51	19.51
Carabus problematicus	19.43	19.43
Carabus problematicus	19.37	38.88
Abax parallelepipidus	15.81	35.24
Pterostichus niger	17.27	56.16
	11.28	46.53
Pterostichus rhaeticus	8.69	64.85
	9.65	56.17

heavy

heavy

Average dissimilarity 94.24% 82.16%

	contrib. %	cum. %
Abax parallelepipidus	12.15	12.15
	10.72	10.72
Nebria salina	10.59	22.74
Pterostichus niger	8.35	19.06
Pterostichus niger	9.42	32.15
Nebria salina	8.26	27.33
Nebria brevicollis	7.92	40.08
	7.42	34.75

Average dissimilarity 92.09% 78.11%

	contrib. %	cum. %
Nebria salina	12.91	12.91
	10.64	10.64
Abax parallelepipidus	10.54	23.45
Carabus problematicus	8.87	19.51
Carabus problematicus	10.46	33.91
Abax parallelepipidus	8.70	28.21
Pterostichus rhaeticus	8.89	42.79
Pterostichus niger	7.21	35.42

Average **similarity** 12.30% 22.27%

	contrib. %	cum. %
Nebria salina	20.62	20.62
Pterostichus nigrita	13.76	13.76
Pterostichus nigrita	10.83	31.45
Nebria salina	12.06	25.82
Carabus problematicus	10.30	41.76
Pterostichus diligens	11.03	36.85
Nebria brevicollis	9.45	51.21
Carabus problematicus	10.81	47.66

S6.4 Results of SIMPER analysis showing most important ground beetle species responsible for similarity within and dissimilarity between altitudinal categories. Black writing = trap scale, red writing = habitat scale.

< 100m

< 100m

Average **similarity** 17.63% 32.91%

	contrib. %	cum. %
Abax paralellepipidus	31.50	31.50
	19.79	19.79
Pterostichus niger	16.16	47.66
	15.99	35.78
Pterostichus madidus	10.57	58.23
	11.23	47.01
Nebria brevicollis	8.68	66.92
Pterostichus vernalis	8.41	55.42

100-200m

Average dissimilarity 86.89% 74.57%

	contrib. %	cum. %
Abax paralellepipidus	18.46	18.46
	10.24	10.24
Pterostichus niger	10.63	29.09
Nebria brevicollis	9.51	19.75
Pterostichus madidus	10.34	39.43
Pterostichus niger	8.78	28.53
Nebria brevicollis	8.52	47.95
Pterostichus madidus	8.41	36.94

100-200m

Average **similarity** 11.48% 26.05%

	contrib. %	cum. %
Abax paralellepipidus	38.04	38.04
	31.31	31.31
Pterostichus niger	17.46	55.50
	18.19	49.50
Carabus problematicus	7.56	63.06
Pterostichus nigrita	8.65	58.16
Pterostichus nigrita	6.48	69.53
Carabus problematicus	7.07	65.23

200-300m

Average dissimilarity 90.70% 80.26%

	contrib. %	cum. %
Abax paralellepipidus	18.38	18.38
	12.55	12.55
Pterostichus niger	12.00	30.38
	9.83	22.37
Nebria brevicollis	10.40	40.78
	9.70	32.08
Pterostichus madidus	9.65	50.43
	9.42	41.50

Average dissimilarity 90.04% 76.23%

	contrib. %	cum. %
Abax paralellepipidus	18.79	18.79
Pterostichus niger	13.32	13.32
Pterostichus niger	16.94	35.73
Abax paralellepipidus	13.02	26.34
Nebria salina	7.13	42.86
	6.43	32.77
Pterostichus nigrita	5.94	48.80
	6.38	39.16

200-300m

Average **similarity** 12.47% 22.15%

	contrib. %	cum. %
Abax paralellepipidus	30.40	30.40
	33.30	33.30
Pterostichus niger	17.49	47.90
	14.37	47.67
Nebria brevicollis	11.50	59.40
	8.57	56.24
Carabus problematicus	9.17	68.57
Pterostichus diligens	8.06	64.30

300-400m

Average dissimilarity 91.61% 79.28%

	contrib. %	cum. %
Pterostichus niger	10.69	10.69
	8.45	8.45
Abax paralellepipidus	10.39	21.08
	8.18	16.63
Nebria brevicollis	10.35	31.44
	7.71	24.34
Carabus problematicus	8.95	40.38
	7.05	31.39

Average dissimilarity 93.01% 79.97%

	contrib. %	cum. %
Nebria salina	15.34	15.34
	13.04	13.04
Carabus problematicus	12.08	27.42
	9.90	22.95
Pterostichus niger	9.48	36.90
	7.85	30.79
Abax paralellepipidus	7.16	44.07
Pterostichus nigrita	6.33	37.12

Average dissimilarity 90.97% 77.17%

	contrib. %	cum. %
Abax paralellepipidus	15.17	15.17
Nebria salina	12.05	12.05
Carabus problematicus	13.82	28.99
Abax paralellepipidus	11.25	23.31
Nebria salina	12.42	41.41
Carabus problematicus	9.81	33.12
Pterostichus niger	10.63	52.04
	9.29	42.41

300-400m

Average **similarity** 11.33% 24.95%

	contrib. %	cum. %
Carabus problematicus	27.23	27.36
	19.53	19.53
Abax paralellepipidus	16.30	43.66
	16.94	36.47
Pterostichus rhaeticus	14.94	58.60
	13.18	49.65
Pterostichus niger	12.29	70.89
Pterostichus nigrita	10.97	60.62

> 400m

Average dissimilarity 91.18% 79.27%

	contrib. %	cum. %
Abax paralellepipidus	11.47	11.47
Pterostichus niger	8.14	8.14
Pterostichus niger	10.40	21.86
Abax paralellepipidus	8.04	16.18
Nebria brevicollis	9.30	31.16
Nebria salina	7.11	23.29
Carabus problematicus	7.44	38.60
Nebria brevicollis	6.95	30.24

Average dissimilarity 90.72% 76.06%

	contrib. %	cum. %
Nebria salina	13.50	13.50
	11.86	11.86
Abax paralellepipidus	12.45	25.95
Carabus problematicus	7.88	19.74
Carabus problematicus	10.42	36.36
Abax paralellepipidus	7.80	27.54
Pterostichus niger	8.50	44.86
Pterostichus rhaeticus	7.14	34.68

Average dissimilarity 91.08% 76.98%

	contrib. %	cum. %
Abax paralellepipidus	16.42	16.42
Nebria salina	10.98	10.98
Nebria salina	12.02	28.44
Abax paralellepipidus	10.19	21.17
Carabus problematicus	11.20	39.64
	9.56	30.74
Pterostichus niger	10.45	50.09
	8.30	39.04

Average dissimilarity 88.52% 70.66%

	contrib. %	cum. %
Abax paralellepipidus	13.43	13.43
Pterostichus rhaeticus	10.51	10.51
Pterostichus rhaeticus	12.83	26.26
Nebria salina	10.40	20.91
Carabus problematicus	12.59	38.86
Abax paralellepipidus	10.09	31.00
Nebria salina	11.92	50.78
Carabus problematicus	9.03	40.03

> 400m

Average **similarity** 15.59% 37.58%

	contrib. %	cum. %
Trechus obtusus	20.27	20.27
Carabus problematicus	24.00	24.00
Abax paralellepipidus	20.16	40.43
Trechus obtusus	22.54	46.54
Pterostichus rhaeticus	13.12	53.55
	16.52	63.06
Carabus problematicus	13.00	66.55
Abax paralellepipidus	13.98	77.05

S6.5 Results of SIMPER analysis showing the most important bird species responsible for similarity within and dissimilarity between grazing states.

	light			light-moderate			moderate			heavy		
light	Average **similarity** 41.60%											
		contrib. %	cum. %									
	Wren	30.83	30.83									
	Meadow pipit	25.81	56.64									
	Chaffinch	8.96	65.60									
	Dunnock	5.84	71.44									
light-moderate	Average dissimilarity 57.30%			Average **similarity** 49.36%								
		contrib. %	cum. %		contrib. %	cum. %						
	Meadow pipit	9.35	9.35	Meadow pipit	37.24	37.24						
	Wren	8.66	18.02	Wren	35.26	72.50						
	Dunnock	7.41	25.42	Blackbird	5.06	77.56						
	Swallow	5.37	30.79	Swallow	4.54	82.10						
moderate	Average dissimilarity 60.13%			Average dissimilarity 56.15%			Average **similarity** 52.17%					
		contrib. %	cum. %		contrib. %	cum. %		contrib. %	cum. %			
	Meadow pipit	8.65	8.65	Meadow pipit	11.02	11.02	Meadow pipit	22.53	22.53			
	Wren	6.22	14.87	Wren	7.51	18.53	Wren	19.78	42.31			
	Dunnock	6.04	20.91	Wheatear	6.19	24.72	Blackbird	7.05	49.36			
	Wheatear	5.18	26.10	Skylark	5.82	30.54	Robin	6.70	56.06			
heavy	Average dissimilarity 62.54%			Average dissimilarity 56.49%			Average dissimilarity 56.23%			Average **similarity** 43.36%		
		contrib. %	cum. %		contrib. %	cum. %		contrib. %	cum. %		contrib. %	cum. %
	Wren	8.83	8.83	Wren	12.54	12.54	Meadow pipit	8.67	8.67	Meadow pipit	41.99	41.99
	Meadow pipit	7.80	16.63	Meadow pipit	8.30	20.84	Wren	8.29	16.96	Wren	17.51	59.50
	Dunnock	6.51	23.13	Swallow	5.59	26.43	Wheatear	5.49	22.45	Skylark	7.59	67.09
	Swallow	6.38	29.51	Skylark	5.05	31.47	Blackbird	4.28	26.73	Swallow	60.9	73.19

S6.6 Results of SIMPER analysis showing the most important bird species responsible for similarity within and dissimilarity between altitudinal categories.

	< 100m	100-200m	200-300m	300-400m	> 400m
< 100m	Average **similarity** 45.25% contrib. % cum. % Wren 18.63 18.63 Chaffinch 14.53 33.16 Blackbird 10.06 43.22 Robin 9.91 53.13				
100-200m	Average dissimilarity 64.21% contrib. % cum. % Meadow pipit 6.91 6.91 Chaffinch 6.80 13.71 Swallow 6.20 19.91 Blackbird 5.97 25.88	Average **similarity** 37.71% contrib. % cum. % Wren 28.99 28.99 Meadow pipit 12.58 41.57 Chaffinch 8.89 50.47 Robin 8.04 58.51			
200-300m	Average dissimilarity 73.04% contrib. % cum. % Chaffinch 8.60 8.60 Blackbird 7.18 15.78 Swallow 7.12 22.90 Meadow pipit 7.04 29.94	Average dissimilarity 70.06% contrib. % cum. % Meadow pipit 8.48 8.48 Wren 7.48 15.96 Chaffinch 7.11 23.08 Robin 6.33 29.41	Average **similarity** 50.60% contrib. % cum. % Meadow pipit 53.36 53.36 Wren 27.44 80.80 Skylark 9.24 90.04		
300-400m	Average dissimilarity 68.08% contrib. % cum. % Swallow 8.94 8.94 Wren 8.83 17.77 Blackbird 7.26 25.03 Meadow pipit 6.65 31.68	Average dissimilarity 75.07% contrib. % cum. % Meadow pipit 8.74 8.74 Wren 7.70 16.43 Swallow 7.51 23.95 Chaffinch 7.08 31.03	Average dissimilarity 46.90% contrib. % cum. % Wren 18.26 18.26 Meadow pipit 10.52 28.78 Wheatear 9.39 38.17 Skylark 8.50 46.68	Average **similarity** 57.15% contrib. % cum. % Meadow pipit 70.16 70.16 Wren 17.09 87.25 Skylark 7.81 95.06	
> 400m	Average dissimilarity 72.08% contrib. % cum. % Wren 11.52 11.52 Swallow 9.65 21.17 Blackbird 7.96 29.13 Meadow pipit 7.74 36.87	Average dissimilarity 77.55% contrib. % cum. % Wren 9.79 9.79 Meadow pipit 9.72 19.52 Swallow 7.00 26.52 Robin 6.79 33.31	Average dissimilarity 46.98% contrib. % cum. % Wren 24.94 24.94 Meadow pipit 14.26 39.19 Wheatear 12.44 51.63 Skylark 8.18 59.81	Average dissimilarity 39.40% contrib. % cum. % Wren 31.95 31.95 Wheatear 15.77 47.72 Meadow pipit 14.28 62.00 Skylark 11.32 73.32	Average **similarity** 72.12% contrib. % cum. % Meadow pipit 71.96 71.96 Wren 18.83 90.79

Appendix B

See accompanying book: ‘Farming the Iveragh uplands: A tale of humans and nature’.

‘…there is something final about the highest summit of the Reeks, of Iveragh, of Ireland itself, as if – for the time being at least – there is nowhere else to go and one might as well descend.’

Dermot Somers, The Mountains of Iveragh: A Personal Journey, The Iveragh Peninsula A Cultural Atlas of the Ring of Kerry, 2000