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Mixed herbivore grazing on a lowland heath system: quantifying the collective impacts for conservation management

by

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ABSTRACT

FACULTY OF ENGINEERING AND THE ENVIRONMENT

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Doctor of Philosophy

MIXED HERBIVORE GRAZING ON A LOWLAND HEATH SYSTEM: QUANTIFYING THE COLLECTIVE IMPACTS FOR CONSERVATION MANAGEMENT

By Martin Wilkie

Degradation of terrestrial habitats with high conservation value has resulted in strategic efforts to cease or reverse their declines. Broad habitat management can restore ecological processes and large herbivores can provide ecological function in some terrestrial systems. Following years of decline and fragmentation, owing to factors such as cessation of traditional practices, lowland heathland has become an internationally important habitat with strategic protection. Free-ranging grazing aims to assist in mitigating such losses to habitat and vegetation communities, but quantifying the grazing regime and its associated impacts is necessary to ensure protection of these vulnerable systems. Reviews of herbivore impacts on lowland heath provide detailed evaluations and recognise the absence of experimental assessments and baseline monitoring.

This research aimed to assess ecological activity and impacts (herbage removal, trampling and dunging) of horses and cattle on a lowland heath system to determine their influence on changing vegetation and to inform grazing management. This mixed regime is commonly adopted for restoration of semi-natural habitats but a failure to understand the separate vegetation impacts can be detrimental for the system as a whole.

Behavioural activity was quantified using scan-sampling assessing spatial and temporal variation in behaviour, habitat selection and niche overlap, spatial occupancy and diet. A factorial design was set up to quantify the impacts of herbage removal, trampling and dunging to vegetation separately. Assessments vegetation community composition and architecture in treatment and control areas were undertaken. Analyses incorporated non-parametric and general linear models.

Animals utilised their environments in different ways, varying for feeding and showed high habitat selectivity, based on physiology and foraging strategy primarily. Herbage removal strongly influenced vegetation architecture and heterogeneity owing to selection for graminoids and the plants' competitive traits; effects on other plants were not as well defined due to minimal abundance. Trampling modified the vegetation structure due to reduced canopy density maintaining colonising gaps, but increased graminaceous cover and showed a capacity for lateral expansion. Dunging regime was highly influential for enhancing plant architecture and modified vegetation composition based on nutrient availability and competition. Worming regime was influential on architectural parameters and may be due to retarded dung degradation; further research is required.

The findings contributed knowledge to lowland heath grazing management, validating the use of mixed regimes at low densities, for generating vegetation heterogeneity, for the control of dominating plants and for understanding the impacts of different animal-management practices. Expanding the reach of this research to comparable systems is necessary to develop the knowledge of grazing-management impacts. The work addressed an absence of experimental evaluation on these systems and also illustrated the importance of separately quantifying the impacts of large herbivores.

List of Contents

Chapter 4 The impacts of herbage removal on lowland heath vegetation 63

List of Tables

List of Figures

DECLARATION OF AUTHORSHIP

I, Martin Wilkie, declare that the thesis entitled ‘Mixed herbivore grazing on a lowland heath system: quantifying the collective impacts for conservation management’, and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
- where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
- I have acknowledged all main sources of help;
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
- none of this work has been published before submission

Signed: …………………………………………………………………..

Date:……………………………………………………………………….

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Chapter 1

Introduction

1.1. Habitat loss and biodiversity

The globe has suffered a widespread loss of terrestrial habitat in recent history (Milner-Gulland and Mace, 1998). Many habitats of high conservation value have become severely degraded, often irreversibly. These losses have been explicitly demonstrated at biodiversity hotspots, where half of the world's vascular plants are endemic to just 25 hotspots, once covering 12% of the land's surface but now reduced to only 1.4% (Brooks et al., 2002). Such losses have also been seen in temperate ecosystems, including habitats such as broadleaf forests, which have suffered around 94% conversion to agriculture and logging (Primack, 1998). Despite these alarming figures habitat destruction, fragmentation and degradation continues to increase (Purvis et al., 2000, Kidane et al., 2012, Laurance et al., 2012).

Continued declines have been principally related to anthropogenic activities and include pollution, destruction by urban and industrial development and conversion to higher-yielding agricultural land (Pimm et al., 1995, Begon et al., 1996, Pullin, 2002). Change in land-use is projected to be the primary cause of habitat loss by the year 2100 for terrestrial ecosystems, followed by climate change, nitrogen deposition, biotic exchange and elevated carbon dioxide levels (Sala et al., 2000). The decline in habitat availability and the subsequent species extinctions have significant negative effects on biodiversity.

Biodiversity is defined as the 'the natural variety and variability among living organisms, the ecological complexes in which they naturally occur and the ways in which they interact with each other and with the physical environment' (Gaston, 1996, Redford and Richter, 1999). Biodiversity can be defined in terms of genes, species and ecosystems and can be regarded as having a direct or indirect value. Direct value refers to products that are harvested by people for its consumptive value but not passed through a market (e.g. fuel, food, etc.) or productive use value, harvested and used in the commercial market (e.g. fish, resins, oils, construction materials, ornamental plants etc) (Lindenmayer and Burgman, 2005). Indirect value refers to biodiversity that benefits people without consumption, which is further divided into non-consumptive use value (e.g. protection of water resources, waste disposal, recreation and ecotourism, educational and scientific values etc), option value which is concerned with the value of species and its potential for future economic benefits (e.g. species that can mitigate pollution effects or alleviate disease), and existence value (e.g. protection of wildlife for its intrinsic value) (Chapin et al., 2000, Lindenmayer and Burgman, 2005).

A loss in biodiversity results in a loss in its functional value (i.e. its contribution to the proper functioning of ecosystems), perhaps most clearly illustrated through the capacity for future biological options (Chapin et al., 2000, Dobson et al., 2006). For instance, these options are demonstrated by the potential for biological diversity in estimates of global species number. Best estimates have been calculated at around 14 million species but only around 1.75 million species are known to science so far (Purvis and Hector, 2000). With so little known about biodiversity, its decline equates to a loss of ecological security through the loss of genetics, species and of biological communities or ecosystems as well as a threat to the quality and continuity of human life.

Simultaneous with the loss of habitat, the estimated rate of modern extinction is alarming and far exceeding the natural ‘background’ rate, approximately 1000-10,000 times higher (Purvis et al., 2000, Baillie et al., 2004). And this rate has been increasing. In the last century we saw the end of 20 mammalian species alone and tropical forest, which probably supports the most species, has experienced a rate of loss of about 0.8%-2% per year (Purvis and Hector, 2000, Purvis et al., 2000). Recent research using indicators such as species’ population trends and extinction risk has suggested that the state of global biodiversity is poor and in decline, while pressures on biodiversity (e.g. resource consumption, overexploitation) are increased (Butchart et al., 2010). There is a clear need for evidence-based conservation to determine the scale of human impact on biodiversity and develop practical strategies to prevent extinction.

1.2. Conservation of biodiversity

At a strategic and overarching level much has been done to develop and implement solutions to the problems of habitat and biodiversity loss. Since the Earth Summit in Rio de Janiero (1992) and the Convention of Biological Diversity (CBD, 1993) strategic efforts have been made to cease or reverse the declines across the globe and habitats of high ecological value have received targeted conservation (DOE, 1994, DOE, 1995, Primack, 1998). The CBD set out to establish overarching goals and policies and to coordinate global cooperation on the identified issues. It also provides a framework for conservation, sustainable use of biodiversity and sharing of biological resources (Chapin et al., 2000, Baillie et al., 2004). The Convention formed a formal and international recognition of the state of the planet's biodiversity loss and was a significant turning point for strategic global conservation.

It was also widely recognised at the Earth Summit (1992) that there was a lack of information and knowledge regarding biological diversity (Powledge, 2006) which is integral to make informed decisions for nature conservation. Consequently two major biodiversity assessments followed the Convention: The Global Biodiversity Assessment focussed on determining the scientific understanding of biodiversity and identifying gaps in the knowledge base for future research (Heywood, 1993); and the United Nations Millennium Ecosystem Assessment evaluated the consequences of ecosystem change for human well-being and provided the scientific basis for action required (Powledge, 2006). Jointly these assessments have provided a snapshot of the global status of biodiversity and an indication of the consequences of continued decline, which can directly feed into the conservation actions.

The overall goals and policies set by the CBD are delivered by the signatory countries through their own strategies and Biodiversity Action Plans to tackle to the issues outline previously. In terms of the strategic action in the UK, the Strategy for Sustainable Development published by UK government in 1994 (updated in 1999, 2005) was followed by the launch of 'Biodiversity: the UK Action Plan' (1994) which targeted priority habitats (JNCC, 1994, Price, 2003). A number of species and habitat-specific Biodiversity Action Plans (BAPs) have since been written, providing an important means for setting targets for ongoing strategic management. These Action Plans are driven by international (e.g. EU statute) and national legislation but delivered by the implementing organisations. In an effort to meet the objectives of broad and strategic nature conservation, a translation to the on-the-ground management has been employed at many levels using a number of conservation approaches.

1.3. Nature conservation in practice

Practically addressing the issues surrounding biodiversity and habitat loss can and should be undertaken at many levels. A need for nature conservation may be most clearly demonstrated in small populations when their numbers fall below a critical level and they become vulnerable to issues such as genetic problems, demographic fluctuations or environmental changes. To mitigate these or similar effects species management plans (e.g. endangered keystone or evolutionary unique species), *ex situ* conservation (e.g. captive propagation), protected area management to conserve whole communities, or ecological restoration to re-establish original species or communities are widely utilised (Begon et al., 1996, Hulme et al., 2003, Gordon et al., 2004). These approaches are all valuable for addressing the conservation objectives. The large scale habitat management methods, protected area management and ecological restoration, can provide broad conservation benefits and help to reverse biodiversity losses. These practices to conservation of biological communities may be more effective than species conservation because large numbers of species can be maintained in large enough populations that evolutionary adaption can continue.

Unfortunately protected habitats have been declining in some areas as well as the overall habitat loss. For example a study over 30 years of 60 protected areas across the world showed that around half have seen declines in area and biodiversity (Dhand, 2012, Laurance et al., 2012). The problem has remained a priority and the Strategic Plan for Biodiversity 2011-2020 consists of 20 new biodiversity targets for 2020 termed the Aichi Biodiversity Targets. Among the aims there is a strategic goal ‘to improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity’ and improve the effective management through protected areas (strategic goal C, target 11)(SCBD, 2013).

There are issues of scale in these protected areas. In larger areas, natural processes are able to act out. For example natural dispersal from a parent population (Mace et al., 1998) or heterogeneous grazing patterns which benefit small mammals utilising the ungrazed vegetation, which in turn benefit the predatory birds (Vera, 2009). In smaller, fragmented or degraded habitats interventions are needed where the ecological processes have been hindered (e.g. altered nutrient status, loss of connectivity) (Pywell et al., 2007, Rosenthal et al., 2012, Thomas et al., 2012). In these small areas, the natural systems remain complex and dynamic and the impact of the interventions need to be understood because there may be trade-offs and unexpected negative outcomes.

A number of interventions may be appropriate for these systems and smaller, isolated reserves may require intervention in the form of ecological restoration; although the type of intervention and degree depends on specific conservation objectives. Ecological restoration is defined as the 'process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems' (Jackson et al., 1995). It is the approach to renewing and restoring habitats but also the biodiversity and ecosystem processes. Ecological restoration is applicable for removing introduced non-natives, restoring degraded habitats, or restoring the plants and animals considered natural to an area (Begon et al., 1996).

Across the world, efforts have been made to restore habitats of biological importance that have suffered losses through human disturbance or destruction. In Latin America arid or semi-arid forests have been extensively deforested for agriculture and livestock and have been severely eroded by a lack of appropriate grazing, tillage and fire management (Newton, 2008). The region of Guanacaste, Costa Rica, has undergone widespread and effective restoration (i.e. reforestation) to mitigate the effects of biodiversity loss. The project has employed a number of techniques, such as native species plantations, livestock exclusion and protection from fire (Allen, 1988, Calvo-Alvarado et al., 2009, Griscom and Ashton, 2011). In Europe, the wetlands of Central and Western Europe, have received targeted restorative management as a consequence of the introduction of synthetic fertilizers and extensive drainage for cultivation (Pfadenhauer and Grootjans, 1999). In an effort to reverse the loss of wetland area and enhance species diversity, rewetting, reducing nutrient levels and the use of buffer zones (e.g. reed beds) have been adopted in fen ecosystems (Spieksma et al., 1995, Pfadenhauer and Grootjans, 1999). Restoration of degraded habitats in the UK has been carried out in ecosystems such as semi-improved grasslands or ancient semi-natural woodlands. The restoration of ancient semi-natural woodlands (ASNWs) has been necessary to cease its declines due to abandonment and fragmentation, conversion to coniferous plantations and a decline in traditional practices (e.g. coppicing) (Peterken, 1981, Mitchell and Kirby, 1990). In particular a reduction in habitat quality (e.g. loss of the understorey vegetation that many birds and small mammals utilise), has been a result of a reduction in traditional management, but also competing trees crowding the canopy (Amar et al., 2006, Smart et al., 2007). Restoring coppice rotations (i.e. re-cutting of stem regrowth from stools or stumps) re-establishes the connecting woodland understory and thinning larger mature trees allows light to reach the ground flora and a more diverse vegetation structure to develop (Peterken, 1981, Fuller and Warren, 1993).

Restoration interventions may also make use of mechanical techniques to reduce soil fertility (e.g. turf-stripping and removal) or chemical techniques to restore soil chemistry (e.g. sulphur additions) (Aerts et al., 1995, Diaz et al., 2008) suited to degraded habitat which may have suffered from a loss in species richness and diversity. Less intrusive practices are often more appropriate for ecosystems that have been neglected or there has been a cessation of management often leading to encroachment or dominance of invasive vegetation. These more passive methods include mowing, scrub removal or grazing management (Pywell et al., 2007, Mitchell et al., 2008) which may sensitively and gradually improve and conserve the biological communities being targeted.

Re-introducing large herbivores is an attractive means of restoring the ecosystem processes because of the key role they play in natural and semi-natural systems (van Wieren, 1995, Hobbs, 1996, Rosenthal et al., 2012). Large herbivores have been employed for many years across lowland areas to assist in restoring or managing protected sites dedicated to nature conservation (van Wieren, 1995). These ungulates have been adopted for their ability to control large quantities of dominating plants sensitively, but remove biomass in a more gradual manner than mechanical management (EN, 2005). Herbivore management of terrestrial systems also generates heterogeneous and diverse vegetation, when maintained at the appropriate density (Olff and Ritchie, 1998, Stewart and Pullin, 2008). Indeed, the presence of these animals is considered highly valuable because of the pivotal role once played in mixed arable systems and extensive livestock agriculture such as lowland heath (Webb, 1998) (discussed in more detail in alter sections). On lowland heath the relationships that have co-evolved between the vegetation and the large herbivores are complex and rely on a number of ecological factors, introduced next.

1.4. The ecology of lowland heaths

Heathland is generally characterised by land dominated by ericaceous dwarf-shrub vegetation, typically in north-west Europe where the temperate climate is most suited to the growth of small evergreen plants (Webb, 1986). The distribution of common heather (*Calluna vulgaris*) is closely linked with the marginal western temperate climate (Gimingham, 1972), characterised by mean temperatures between 0°C and 22°C and rainfall of at least 60mm rain in the driest months (Webb, 1986).

Heathland soils are well defined by horizons, or layers, formed by the interactions between underlying rock strata, climate and the vegetation, often termed podsolic (Price, 2003). The A horizon is the topsoil level, a mixture of organic matter and minerals where most plant growth occurs. This is often overlaid with layers of decomposed, partly-decomposed or un-decomposed litter (H, F, L horizons). The ash-grey E horizon is beneath the A horizon, composed of less organic matter and from which alkaline compounds are leached into the B horizon. Between these layers is rich in iron, clay, silica and humus. Horizon C is likely to resemble the parent rock beneath (Webb, 1986, Price, 2003).

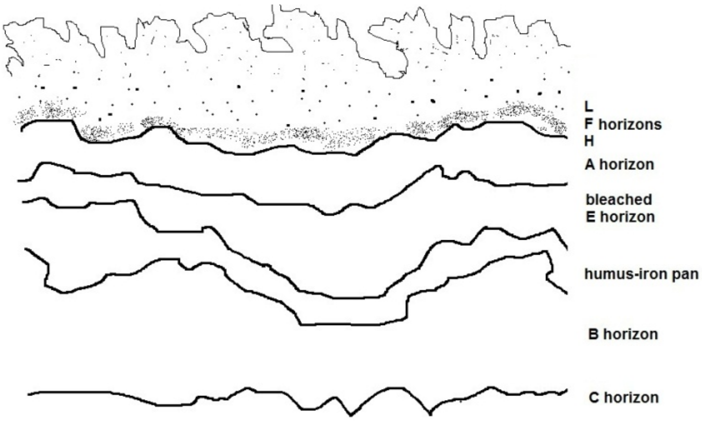


Figure 1.1: Profile of heathland podsol with characteristic horizons

The vegetation of lowland heathland is dominated by characteristic dwarf shrubs growing at low altitudes (typically below 300m above sea level) which favour the dry, acidic, nutrient poor and often podsolised soils (Groves et al., 2012). Composition of the vegetation is highly variable based on soil moisture content and topography (Webb, 1986) and is often interspersed with wetter low-lying basins lined with peat called mires, or acid and mesic grassland, or indeed young woodland in differing phases of succession.

1.4.1. Lowland heath wildlife and ecological value

Lowland heath has huge biological value both nationally and internationally, primarily due to its specialist biota (Price, 2003). The flora and fauna of these systems have become intimately associated with the cultural and historic management, developing specialist niches. A number of rare plant species associated with heathland, such as Eyebright (*Euphrasia* sp.), have seen losses throughout lowland England largely due to a cessation of grazing and degradation of the habitat (Price, 2003). For invertebrates, around 50 percent of the British species in some orders, including dragonflies and true bugs, are supported by the heaths of Southern England (Kirby, 1992 *cited in* Price, 2003). Similar trends are present for vertebrates, supporting populations of amphibians and reptiles such as the palmate newt (*Triturus helveticus*) and sand lizard (*Lacerta agilis*), utilising the diverse habitat mosaic. Heathland is the only habitat in which all six native reptile species can be found (Lake et al., 2001). Few species of avifauna are permanent residents on heathland, however a number of internationally protected species (e.g. Annex I species in the European Birds Directive (79/409/EEC); Dartford Warbler *Sylvia undata*, Woodlark *Lullula arborea*, Nightjar *Caprimulgus europaeus*) with very specific habitat and dietary requirements, are supported and widely suited to the invertebrate prey populations that inhabit heath (Hartley et al., 2003).

The UK Biodiversity Action Plan, launched in 1994 for priority habitats (and species) following the Convention of Biological Diversity (1993) (JNCC, 1994), targets lowland heath in an attempt to cease and reverse the declines observed in biological communities over centuries (DOE, 1994, Maddock, 2008). Among the legislation the EC Habitats Directive (92/43/EEC) also creates a European network of protected areas known as ‘Natura 2000’, including Special Areas of Conservation (SACs) (Annex I) (Price, 2003, Bell and McGillivray, 2006). European dry heaths, northern Atlantic wet heaths, temperate Atlantic wet heaths and dry Atlantic coastal heaths are Annex I habitats. National legislative protections include the Wildlife and Countryside Act (1981) and the Countryside and Rights of Way Act (2000) which strengthen statutory designations such as Sites of Special Scientific Interest (SSSI) (Bell and McGillivray, 2006) a large proportion of which are heathlands.

1.4.2. Development of lowland heath

Heathland was developed from extensive woodland clearances and changing climatic conditions, thereafter sustained by continual low-level management such as sedentary pastoralism including extensive grazing. Prior to the forest clearances the soils were likely to have been derived from poor parent materials and at this time (c. 4000 years before present) the wetter oceanic climate left the soils and forest in a delicate balance (Gimingham, 1972, Webb, 1986). The activities such as forest clearances or the prevention of regeneration could have altered this balance, initiating acidification and podsolization, through removal of nutrients from the cycle (Webb, 1986). *Calluna* was likely to have been present in the flora, on the nutritionally-poor soils, prior to this change which resulted in the subsequent expansion of heath (Webb, 1986). The expansion of Ericaceous pollen is also observed in the pollen record when open heath developed following a reduction in forest cover (Gimingham, 1972).

The influence of man on heathland development is shown in the evidence of pollen analysis, microscopic charcoal, radiocarbon data, soil profiles and archaeological evidence (Price, 2003, Groves et al., 2012). The large-scale clearances of forest for livestock in the Neolithic period provided opportunities for heathland species to spread, the removal of these trees arresting the succession of the vegetation and promoting the growth of dwarf-shrub communities. Such clearances continued throughout the Bronze and Iron Ages (Webb, 1986, Price, 2003) and open heathland was maintained through continual practices including turf removal for fuel, cutting for animal fodder and extensive grazing (Webb, 1998).

Heathland was once a cultural habitat spreading across the Atlantic regions of Western Europe and extending to several million hectares (Webb, 1998), it was at its most expansive in the medieval period of Britain demonstrated in the paleoecological evidence in southern England (Groves et al., 2012). In this region lowland heath is present from Cornwall to East Anglia and the charcoal and pollen records have shown that the scale and nature of human activity has remained an important factor for vegetation change

(Groves et al., 2012), a highly influential factor for the expansion and decline of this habitat.

1.5. Threats and the decline of lowland heath

The once wide expanses of lowland heath have changed over time, becoming isolated and fragmented, and its vegetation altered due to changing human activities. Today around 14% of the total area of this habitat in Europe exists across the southern regions of England (Groves et al., 2012). Habitat destruction and degradation are responsible for the loss of this ecologically, culturally and historically important habitat. Since 1800 there have been losses of around 80 per cent (Price, 2003) due to destruction such as direct conversion to agriculture, forestry or urbanisation, while factors responsible for degradation include enrichment of the soil as well as the cessation of traditional and once common practices (e.g. extensive grazing) (Mitchell et al., 2008).

Habitat destruction has been a major factor in the decline of lowland heath. Land management in northern Europe had considerable affects on heathland area at the turn of the 19th and 20th century with the introduction of synthetic fertilizers, combined with reduced common land grazing. In an effort to make agriculture more efficient and increase productive yield of livestock, heathland agriculture became undesirable and uneconomical (Gimingham, 1972). It was at this point that large areas of heath were transformed by mechanized methods and fertilisation from acidic nutrient-poor habitat to improved farmland with limited biological diversity (Bokdam and Gleichman, 2000). In areas where conversion to forestry was adopted, similar losses of habitat were observed. British forest plantations became a widespread and productive industry on afforested heathland, in the upland heaths of Scotland but also in lowland areas such as the New Forest in central southern England. Alternatively, in developing areas of the UK, lowland heath was seen as a barren landscape and urbanisation threatened lowland heath following the expansion of towns and cities in the 1950s, particularly in southern England. Between 1978 and 1987 there was a loss of around 50 per cent of Dorset heaths due to planning developments (Rose et al., 2000, Price, 2003). In southern England many of the fragmented areas of heath are located in largely populated regions and exist as smaller sites.

Degradation of many lowland heaths with high conservation value has also resulted from increases in fertility due to nitrogenous emissions associated with fossil fuel combustion or agriculture. The deposition of these pollutants has altered nutrient cycling processes, plant growth and community composition (Barker et al., 2004). In the Netherlands, loss of *Calluna*-dominated areas is directly linked to nitrogen deposition, and evidence suggests similar trends in Britain (Rose et al., 2000, Hartley and Mitchell, 2005). Field experiments have indicated that such depositions have increased the rate of invasion from dominating grasses (e.g. *Deschampsia*), increasing the concerns about a long-term shift in vegetation balance (Barker et al., 2004) and perhaps an increased need to control these plants with grazing.

Degradation may also be due to the absence of ongoing management. The large scale abandonment of heaths has altered their vegetation composition and structure increasing scrub invasion and succession to woodland. Moore (1962) *cited in* Gimingham (1972) presented the progressive decline from 1811 to 1960 of lowland heath in Dorset and Hampshire, predicting that ‘in 30 years or less no heath will remain except that protected as nature reserves’ (Gimingham, 1972). Historic practices such as cutting of turves and peat for fuel and fertiliser and burning mature heath to generate young forage once maintained the lowland heath in its impoverished and sub-climax successional state. These collective practices also halted the succession of scrub and prevented reversion to woodland, while grazing stock in outlying heaths meant the land was worked in a manner that was consistent with the terrain in a low intensity approach to gain the highest yields (Webb, 1998).

The loss of the low-level continual practices as well as the removal of grazing have been the greatest drivers for changing vegetation assemblages and degradation (Webb, 1998). The removal of herbivores has been damaging by allowing scrub encroachment, such as in the New Forest where a massive reduction in cattle and ponies from around 2200 and 3000 in the late 1800s to approximately 1000 and 750 in 1940 was observed (Tubbs, 1968 *cited in* Lake *et al*., 2002). Such dramatic reductions in numbers have not occurred in the upland areas of England, Wales and Scotland where sheep grazing on heaths remain important and indeed overgrazing has become an issue (Hester and Baillie, 1998, Hulme et al., 2003, Pakeman and Nolan, 2009). In other lowland areas common lands were no longer utilised by the 1960s, such as many heathland commons in Pembrokeshire which was followed by declines in habitat condition (Evans, 1989). Similar changes to vegetation communities in North Europe, such as southern Sweden, Denmark, Belgium, Holland and Germany can be attributed to reductions in grazing over the last century (Gimingham, 1972, Bullock and Pakeman, 1997) demonstrating the role the animals play in maintaining the biological communities.

1.6. Traditional grazing management

Grazing plays a functional role in maintaining the vegetation in a phase of sub-climax succession on lowland heath. The historic grazing regimes and practices continually maintained the heath in a seral, or sub-climax, state, halting reversion to woodland (Gimingham, 1972). Continuous herding and maintaining livestock at a low density transferred nutrients from the heath to cultivated land and resulted in a nutrient-poor acidic substrate with a diverse vegetation community (Webb, 1998).

Across Northern Europe the use of small stock was customary, especially sheep, routinely left to graze all year round and frequently shepherded (Lake et al., 2001). Cattle were generally grazed on remote heaths but stabled at night to collect their arisings especially in the winter months when available fertilizer was at a minimum. Horses and ponies were grazed continually although there is limited evidence of the latter in England (Webb, 1998). Free-ranging grazing on distant heaths allowed arable crops to be cultivated near to the settlements, and thus the land to be managed in the most economic manner (Lake et al., 2001). Over thousands of years, cultivation and stockmanship lead to a highly efficient use of the landscape, critical to a viable existence in an age prior to modern agriculture. For example, in the Dorset heaths, cattle were primarily grazed on distant heaths or common lands only being brought to neighbouring more nutritious lands for fattening up (Tubbs, 1968). Similar practices were present in other parts of Europe such as Portugal, moving flocks of sheep and goats over great distances to superior pasture which achieved low-density grazing requiring relatively lower inputs of labour (Webb, 1998).

The traditional stocking regime and stocking rate on lowland heath has been scarcely recorded in southern England (Lake et al., 2001), but mixed grazing regimes were historically stocked on lowland heath (such as the New Forest) at an average of 0.11 cattle and 0.18 ponies per hectare (Tubbs, 1997 *cited in* Lake et al, 2001)(Putman, 1986).

These approaches were part of a cultural landscape which has been lost in much of the lowland heath since a change in agricultural practice, other than in places of recreation and ecological value such as the New Forest or in western Norway (Tubbs, 1991, Webb, 1998). By their nature, the traditional practices provided a refined and efficient approach to managing the land and have been extensively revived in modern habitat management.

1.7. Restoration and grazing management

The reinstatement of practices such as grazing, once used regularly in pastoral agriculture, has been instrumental in modern conservation management to achieve biodiversity objectives for priority habitats (van Wieren, 1995, Kimball and Schiffman, 2003, Loucougaray et al., 2004). Grassland, wood pasture, floodplain, coastal marshes and heathlands all require some level of grazing to maintain structure and composition of the vegetation. It is this composition and structure which play such an important part in maintaining populations of flora and fauna (EN, 2005).

These once common techniques have been reintroduced into lowland heath as a method of restoring the ecological processes and halting the process of natural change which occurs in heathland vegetation (Webb, 1986). Historical grazing on larger outlying heaths has been mirrored by extensive free-ranging grazing in modern habitat management (Bokdam and Gleichman, 2000) and continual year-round grazing is often adopted today as was customary in the past, although not exclusively (Webb, 1998, Lake et al., 2001). The mixed regimes, utilised as a practical and efficient use of the land are now common in conservation grazing, while the low stocking numbers which are now employed were a product of necessity to gain the highest livestock yields with the lowest inputs of labour (Webb, 1998). Traditional breeds are often selected in conservation sites for their tolerance of nutrient-poor forage and hardiness to weather conditions (Lake et al., 2001).

There has been widespread and growing support for adopting long-term grazing regimes for maintaining vegetation communities for ecological restoration (Bokdam and Wallis de

Vries, 1992, Hayes and Holl, 2003) and on lowland heathland (Bullock and Pakeman, 1997, Lake et al., 2001, Newton et al., 2009). Studies have documented the influence of herbivore activity upon vegetation structure (Bokdam and Wallis de Vries, 1992, Hayes and Holl, 2003) and maintaining and enhancing biodiversity through increased spatial heterogeneity (Fleurance et al., 2001). Contrastingly, some evidence has suggested that long-term grazing is counterproductive, reducing species and structural diversity (e.g. by increasing grazing-tolerant species in grassland) (Bokdam and Gleichman, 2000, Kimball and Schiffman, 2003), although other potential drivers were recognised. Other issues that have been documented are over- and under-grazing, for instance overgrazing on heath can lead to degradation of sensitive habitat (Welch and Scott, 1995, Pakeman and Nolan, 2009) and similarly under-grazing can alter the competitive balance of some species allowing fast-growing and dominating plants to invade (Mitchell et al., 2008).

Grazing regime (e.g. mixed or single animal species, stocking rate, grazing durations etc) has been documented as a determining factor for habitat architecture (Sternberg, 2000) and vegetation composition (Rook and Tallowin, 2003, Scimone et al., 2007). The differences in dental and digestive physiology of the grazers are important for governing the impact to grazed communities, as is body size (Sneddon and Argenzio, 1998, Rook et al., 2004). Between horses and cattle, for example, intake and forage prehension is critical for the selective grazing of swards (Hongo and Akimoto, 2003) which can be influential for governing physical vegetation changes (Lake et al., 2001).

Grazing regime has been important for developing grazing management for the restoration of sensitive habitats (Lake et al., 2001), not excluding other drivers such as climate or site conditions. However understanding the ecosystem function and baseline monitoring of the impacts to the vegetation, should be regarded as key for providing predictive knowledge (Bokdam and Gleichman, 2000).

1.8. Foraging behaviour, ecosystem function and vegetation change

Grazing herbivores influence plant communities through a number of processes which are related to foraging behaviour. Foraging behaviour is the mechanism for large herbivores to maintain their energy and nutrient requirements and their activity directly relates to the impacts discussed later. Feeding and resting are likely to comprise the majority of the animals' behavioural activity (van Dierendonck et al., 1996), but other behaviours are likely to be influential, such as social interactions with conspecifics (Dumont and Boissy, 1999) or predator vigilance (Kie, 1999). Crucially, digestive physiology regulates foraging (e.g. in ruminants) (Sneddon and Argenzio, 1998) and foraging strategy, or the patterns exhibited to obtain energy and nutrients to survive and reproduce (Laca and Demment, 1996) is an equally important driver. The acquisition of nutrients and energy is critically related to the spatial and temporal distribution of resources (Wallis de Vries, 1996), revealing the complex dynamics between the animals and their environment. A detailed introduction to foraging behaviour in included in Chapter 3 of this thesis.

Processes which have a direct influence on plant communities include plant consumption, regulation of competing species, modification of nutrient cycling or disturbance of soils (Ritchie and Olff, 1999). Herbivores govern structure, competitive balance and community composition which influences the functionality and productivity of an ecosystem (Archer, 1996). For example, even if a small proportion of biomass is consumed, the effects can be important if relatively rare species then become dominant and the herbivore therefore has become critical for influencing plant composition and possibly succession (Ritchie and Olff, 1999).

The functional relationships between herbivores and plants has been widely studied (Hutchings and Gordon, 2001, Palmer et al., 2003, Hartley and Mitchell, 2005, Critchley et al., 2008). A delicate balance may be observed through specialisations in some plants, such as the particular conditions within lowland heath which may rely on continuing disturbance like suppressing competing grasses. The interactions between herbivores and other assemblages are also documented, such as invertebrates (Dennis et al., 1997), reptiles (House and Spellerberg, 1986), and birds (Evans et al., 2006), based on vegetation suitability (e.g. sward height, structure and cover). These were not assessed in this thesis.

Three mechanisms are critical for modifying the vegetation: herbage removal, trampling and dunging. These mechanisms alter plant growth, reproduction and the competitive balance within a community (Crawley, 1983, Cole, 1995a, Ball et al., 2000, Kohler, 2004). Herbage removal is understood to be highly influential for vegetation change due to the direct modification of plants or plant parts (Lemaire and Chapman, 1996, Olff and

Ritchie, 1998). Similarly, the physical modification of vegetation by trampling has been observed to enhance vegetation structure, open gaps for colonisation (Cole, 1995a, Pavlu et al., 2007) and alter species composition (Kobayashi et al., 1997). Finally, dunging regime has been regarded as influential for vegetation based on an increase of nutrients (Gough et al., 2000) and by the respective nutrient availability from different animals (Sneddon and Argenzio, 1998, Rook et al., 2004).

It is via these mechanisms that herbivores can also generate top-down effects or trophic cascades in the food chain. For instance, there may be a reduction in the biomass of primary producers (e.g. plants) through herbage removal, especially in the absence of control by a higher trophic level (e.g. a predator) (Jefferies, 1999), which may be of benefit to meet some conservation objectives. These downward-driven trophic effects may also be negative, for example if localised cascading effects occur through over-grazing, degrading trampling or nutrient input if stock numbers are too high, altering the habitat's suitability (Gordon et al., 2004). In terrestrial systems, the overall effects of such trophic cascades are often dissipated due to the heterogeneous and species-rich communities, but in the absence of negative-feedback mechanisms (i.e. predation or disease), the system may become destabilised and a new equilibrium established (Jefferies, 1999). There may not be the capacity for ecological processes to operate in small, isolated or fragmented systems, unlike large-scale systems, but large herbivores can restore function if managed appropriately (Rosenthal et al., 2012). Evaluation of the separate mechanisms is necessary.

1.9. Separating the effects of herbivores

As described in the work by Kohler et al. (2004) there is often a simplification of the herbivore effects into a measure of 'grazing' (Kohler, 2004, Kohler et al., 2004). Three mechanisms - herbage removal, trampling and dunging - are the principal disturbance factors of large herbivores (Rook and Tallowin, 2003, Gillet et al., 2010) and have significant individual small-scale impacts (Kohler, 2004). Many studies have separately quantified the effects of herbage removal (Milchunas and Lauenroth, 1993, Bullock et al., 1994), trampling (Cole, 1995a, Kobayashi et al., 1997) and dunging (Dai, 2000, Gillet et al., 2010). A few have recognised the gap in the knowledge and examined the mechanisms separately in the same study, in mountain pastures of Switzerland (Kohler, 2004, Kohler et al., 2006b) and within upland areas of Scotland (Oom et al., 2008). The collective assessment of the mechanisms in Swiss pastures (Kohler et al., 2004) indicated herbage removal and dunging governed short term plant dynamics, reducing species richness by dominating grasses, but vegetation response to trampling was weak. In the short-term, plant changes were clearly demonstrated by animal impacts, while in the long-term impacts may begin to reveal successional processes (Kohler, 2004).

An experimental evaluation of the fine-scale vegetation changes is absent in lowland heath and has only been experimentally tested for each mechanism (Bullock et al., 1994, Bokdam and Gleichman, 2000, Britton et al., 2000b, Barker et al., 2004) or reviewed based on management approaches (Bullock and Pakeman, 1997, Lake et al., 2001). An experimental assessment of herbage removal, trampling and dunging separately but within one experimental study would enable the investigation of the comparative impacts of each of the mechanisms. Despite these mechanisms being highly related, it is essential to experimentally-separate them to quantify the actual vegetation changes because each is highly influential in its own right. In grassland, for example, trampling may be important for allowing species colonisation of less diverse grasslands, while in more diverse grassland communities herbage removal may dictate the balance of plant species (Rook et al., 2004). It would be impossible to determine the driving mechanism for vegetation change if they were not separated.

1.10. Synthesis

Against a backdrop of biodiversity loss and habitat degradation globally, European conservation efforts are focussed upon key habitats such as lowland heathlands. These habitats are widely acknowledged to be of high conservation value owing to their specialist flora and fauna, confined to these systems and evolved under traditional land use (Maddock, 2008, Rosenthal et al., 2012). Following years of loss and degradation there has been a recognised need for strategic interventions (Newton et al., 2009). The lowland heath of central Western Europe is a unique and rare habitat both ecologically and culturally and has become a priority for biodiversity action. In the last 200 years lowland heath has come under growing threat from degrading human activity, becoming rare and threatened (Webb, 1998, Diaz et al., 2008). The changing attitudes in the latter decades of the twentieth century formally recognised the importance of these heathlands and protective legislation followed (e.g. Annex I habitat of the Habitats Directive (92/43/EEC)). Considerable steps were taken in an effort to maintain the remaining lowland heathlands by the governing States, landowners and conservation organisations, and manage them appropriately. Grazing management was recognised as a technique to maintain the biodiversity value of this habitat type.

The complex effects of herbivores have been documented and reviewed (Bullock and Pakeman, 1997) and there continues to be conflict about their benefits and disagreement in the literature regarding the impacts on some key communities (Newton et al., 2009). There has been also a scarcity of baseline monitoring and experimental evidence quantifying the impacts of grazers on lowland heath vegetation (Lake et al., 2001, Newton et al., 2009). The documented evidence has often been limited to a single mechanism, grazing, evaluating all the complex processes as a single effect (Bokdam and Gleichman, 2000); as recognised in some studies of vegetation change (Kohler, 2004, Oom et al., 2008). The actual impact of grazers on vegetation is a collective effect of three mechanisms (herbage removal, trampling and dunging) (Kohler, 2004, Oom et al., 2008).

Despite the work examining the collective, but separate, impacts of herbivores on vegetation (Kohler, 2004, Kohler et al., 2004) there is a lack of experimental evaluation of all three impact mechanisms on lowland heath, other than investigations of ‘grazing’ (Putman, 1986, Bullock and Pakeman, 1997, Bokdam and Gleichman, 2000). Furthermore, few studies have comparatively assessed the respective impacts of mixed grazing low-intensity regimes concurrently at an empirical level (Edwards and Hollis, 1982, Putman et al., 1991, Loucougaray et al., 2004, Cosyns et al., 2005).

Measuring the ecological impacts of large ungulates can validate the effectiveness of traditional practices in modern habitat conservation, verifying if the regimes do assist in restoring the ecological processes that lowland heath relies on. Furthermore, quantifying the impacts can provide evidence and predictive knowledge for designing effective grazing systems for conservation management (Bokdam and Gleichman, 2000).

In this thesis, spatial and temporal trends were examined by an observational study of large herbivore activity in a lowland heath protected area. The ecological impacts of herbage removal, trampling and dunging were separately assessed for both cattle and horses.

1.11. Statement of Research Objectives

In this thesis a direct quantification of the activity and the impacts of grazing herbivores on a lowland heath system was undertaken in order to determine the influence of these animals on the vegetation. The findings would be used to assess traditional grazing management and inform decisions for conservation grazing, such as the control of dominating grasses in this vulnerable habitat. An experimental approach was adopted for much of the research, building on the work of Kohler et al (2004; 2006).

The overall aim of the research was to evaluate the multiple impacts of large herbivores upon a lowland heath system, through assessment of the animals and the vegetation on grassland, mire, heath and woodland. These evaluations were set into the context of meeting biodiversity goals by improved grazing management.

Specific research objectives:

1) Quantify and compare herbivore behavioural activity in the heathland landscape and assess the spatial and temporal use through the seasons to determine their influence on the vegetation.

2) Quantify the architectural and biological impacts to the vegetation within the heath system and its associated habitats (grassland, mire, heath and woodland), specifically through the key mechanisms:
    - Herbage removal (controlling for trampling and dunging)
    - Trampling (controlling for herbage removal and dunging)
    - Dunging

3) Make recommendations to inform the conservation management of lowland heaths based on the knowledge obtained and from the identified underlying processes and dynamics occurring between herbivores and vegetation.

This thesis is composed of seven chapters. Chapters 1 and 2 are introductory providing background and general methods. In Chapter 3 the behavioural activity of the grazers was evaluated by quantifying the spatial and temporal trends of these animals through the seasons on the lowland heath system. The subsequent Chapters 4, 5 and 6, used field experiments to focus on the architectural and biological changes to the vegetation brought about by the presence of large herbivores through each separate impact mechanism (herbage removal, trampling and dunging). Chapter 7 of this thesis provides discussion and recommendations.

Chapter 2

General methodology

This chapter provides an overview of the study site, grazing regime and sampling methods. Each chapter will describe the specific methods and procedures for sampling as well as details of analyses relevant to that chapter. The assessment of vegetation communities and their architectural parameters throughout the succeeding experimental chapters (Chapters 4, 5, 6) are comparable and are outlined below.

2.1. Study site

The study was conducted on a lowland heath, in north-east Hampshire, UK, Eelmoor Marsh Site of Special Scientific Interest (SSSI)(Appendix 1), which was historically part of a larger system of lowland peat moor (51.274 N; 0.796 W). Some parts of the site are designated as Site of Interest for Nature Conservation (SINC) and also form part of the Thames Basin Heaths Special Protection Area (SPA) under the EC Birds Directive (79/409/EEC) for three species listed in Annex I, namely Dartford Warbler (*Sylvia undata)*, nightjar (*Caprimulgus europaeus)* and woodlark (*Lullula arborea).*

The site is low-lying at an elevation of c.70m above sea level. The site is a naturally wet area, with several seepages and springs forming the source of an adjoining watercourse, although higher areas are drier (see habitats description s*ection 2.2.*). The soils are quite variable across the site, ranging from yellowish brown fine loamy sand through to black wet peat of varying thicknesses. The sandy soils vary in soil moisture content (dry to wet), soil organic matter (loamy sand to humus-rich peat) and pH (highly acidic to neutral). The site is situated on underlying Bracklesham Beds with the elevated north and west on Barton Sand Beds which are capped in places by Downwash Gravel, both typically fine sands with clay-rich material at depth (Allen, 1999)

Eelmoor Marsh experiences an average annual total sunshine of 1510 hours, with the monthly average varying from 42 hours in December to 206 hours in June. The mean daily temperature ranges from 4°C in January to 21.5°C in July and the mean annual rainfall is 670mm (Hall et al., 2009).

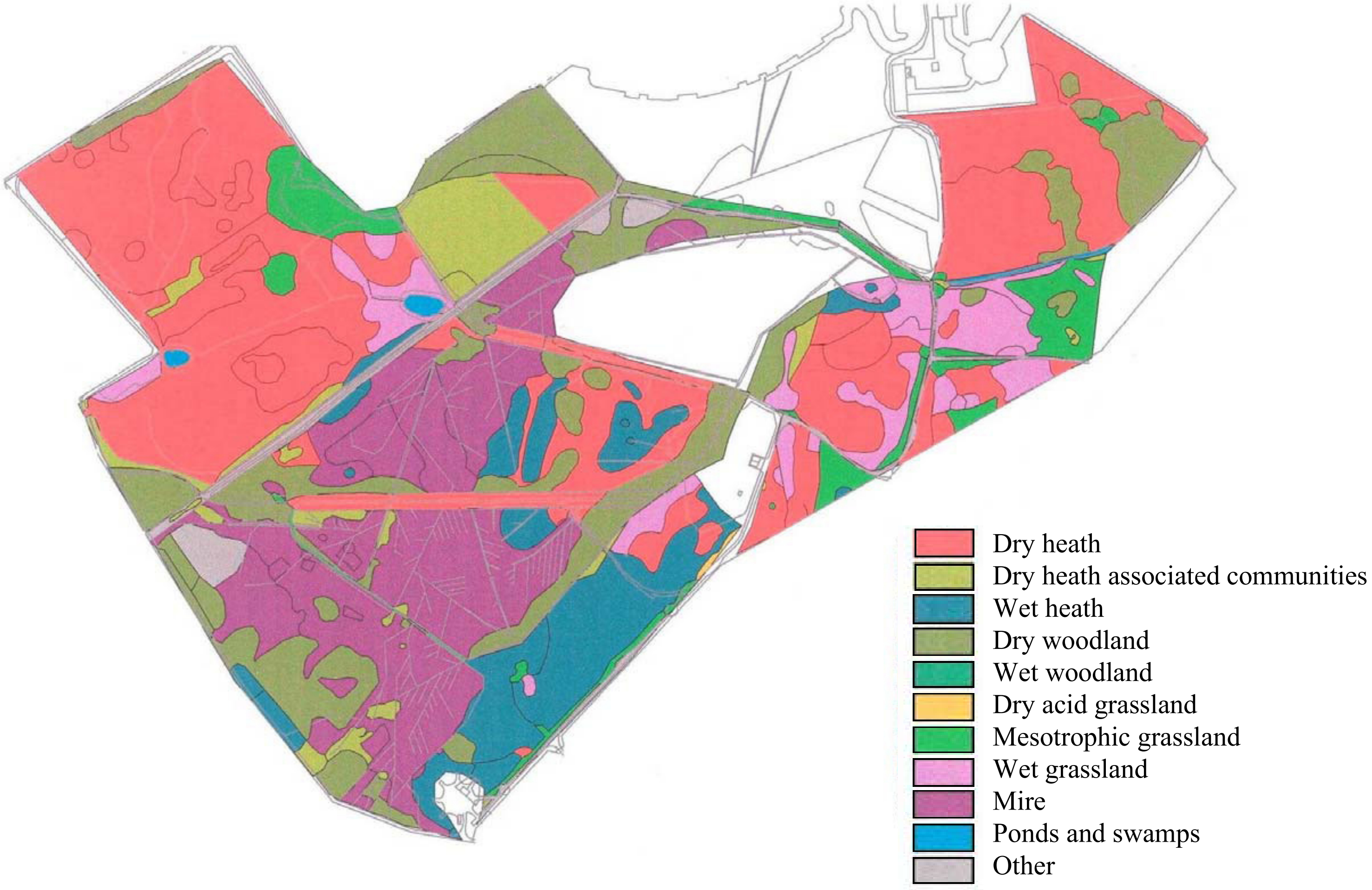


Figure 2.1: Vegetation communities of Eelmoor Marsh from NVC and Condition assessment report, Sanderson (2003). © Natural England copyright. Contains Ordnance Survey data © Crown copyright and database right 2003

In terms of formal management, the site is managed under a five-year management plan which establishes a number of conservation aims, including to: (i) maintain, increase and enhance valued habitats; (ii) maintain or increase populations of valued species; and (iii) control, reduce or remove alien and invasive species (Hall et al., 2009). The site is managed based on the vegetation communities and management compartments.

2.2. Habitats and vegetation communities

The landscape is diverse and broadly dominated with dry and humid-wet heath (vegetation dominated by *Calluna vulgaris* and *Erica* sp.), mixed secondary woodland (deciduous and coniferous with ground flora including *Rubus* sp., *Pteridium* sp. and *Betula* sp.), mire (vegetation dominated by *Molinia caerulea* and *Myrica gale*) and open grassland (acid and neutral). Although heath covers almost 30 percent of the site, it is interspersed with scrub (e.g. *Betula pendula* and *Pinus syvestris*) and associated mire communities with dominating purple-moor grass (e.g. *Molinia caerulea*). Flowering and fruiting of vegetation occurs between April and October. Table 3.1 in Chapter 3 displays the detailed habitat proportions for the site divided into dry and wet heath, the north and south respectively (habitat classification map displayed in appendix 2). This division of the site was appropriate for the approach for assessing spatial-temporal activity in Chapter 3, but the remaining chapter examine the site as a whole.

A network of watercourses means adjacent habitats are largely humid heath to wet bog and mire. The south and east are low-lying and comprise of open mesic grassland, secondary woodland and humid heath. The lands to the north and west (c.90m) are much drier and dominated by acid grassland and *Calluna*-dominated heath.

Vegetation mapping of the site identified a total of 68 vegetation communities and sub-communities (Hall, 2008, Hall et al., 2009) based on the National Vegetation Classification (NVC) (Rodwell, 1991, Rodwell, 1992) (Figure 2.1). Vegetation communities of interest include dry heath (H2a), humid heath (H2c), herb-rich heath (H8b), open wet heath (M16c), *Molinia* grassland (M24c), parched acid grassland (U1d), and valley bog (M21).

A general classification of vegetation communities were originally devised to assist habitat management for the entire site by summarising the dominant vegetation, but also to target management of key vascular plants on the protected reserve (Appendix 3). The broad communities were also used extensively in the initial phases of vegetation mapping prior to recording livestock occupancy (Chapter 3). These general classifications were identified as:- dry heaths and humid heaths which included *Calluna*-dominated habitats and *Agrostis*-dominated heath; dry heath associated communities such as *Molinia*-dominated heath, gorse and bracken dominated heaths; dry acid grasslands, mesic grasslands (improved, semi-improved and rank grassland); wet heaths; wet grasslands; mires (valley bog, *Molinia*-dominated mire, fen); wet woodlands; riverine woodlands; mesotrophic ponds and swamps; dry woodland; and other (bare ground) (Sanderson, 2003). For the purposes of the experimental chapters the habitats were broadly grouped and classed as grassland, heath, mire and woodland.

2.3. Stocking regime

The site was stocked with small groups of two species: 10 Scottish Highland cattle (*Bos taurus*) and 6 Przewalski's horses (*Equus ferus przewalskii*). All animals had been on site for more than four-years and were free-ranging. The animals were employed at stocking densities of 0.12 and 0.08 livestock units per hectare (LU/ha) for cattle and horses respectively. This is the reported stocking density is for Chapter 4, 5 and 6. Chapter 3 reported stocking density differently at 0.25 LU/ha and 0.18 LU/ha (dry heath and wet heath) due to the investigation of these habitat types (north and south, respectively). These stocking densities in Chapter 3 were for the mix of horses and cattle on each habitat type. Animals were not fed any supplementary feed unless the environmental conditions dictated (e.g. heavy snow), and veterinary interventions were only carried out when required. Animals were not treated with antihelmintic medications and were monitored closely for overall body condition with faecal screening undertaken at regular intervals, according to recommended conservation grazing practices (Tolhurst, 2001).

2.4. Experimental design

In chapters 4, 5 and 6, a balanced factorial design was established in the four broad habitats (open grassland, heath, *Molinia*-mire, secondary woodland). The design is approximately equal across the experimental chapters (4, 5, 6) assessing the effects of impact treatment and controls after the experimental period. The factorial design set out to address the specific research objective 2 (*section 1.11*) and quantify the architectural and biological impacts to the vegetation within the heath system and associated habitats, specifically through the key mechanisms: herbage removal, trampling and dunging. The herbage removal design could not exclude the effects of trampling as recording natural foraging did not make this possible, but within the logistical constraints of field experimentation this was accepted. The trampling design could minimise the effects of herbage removal through positioning of experimental plots and surveillance (detailed in each respective chapter). Three replicate blocks were located in each habitat, fenced in May 2008 to September 2011 as controlled experimental exclosures. This design differed in Chapter 6 as all the dunging factor treatments and controls were all enclosed within the plots, and so the other mechanisms were not influential. The blocks excluded livestock, but other herbivores such as roe deer and rabbits were not controlled as they had minimal presence, based on field observations. The exclosures were constructed from untreated spiked timber posts with two bands of wire between the posts.

2.4.1. Vegetation sampling

Within the field blocks, $1m^2$ quadrat sub-plots were sampled at the end of the experimental period measuring the vegetation parameters to address research objective 2 (*section 1.11*). Research objective 3, to make recommendations to inform the conservation management of lowland heaths based on the knowledge obtained and from the identified underlying processes and dynamics occurring between herbivores and vegetation (*section 1.11*), was also partly addressed by examination of the vegetation changes. Standard measures of vegetation parameters were carried out for each of the experimental chapters including biological (species composition) and architectural (sward height, structural heterogeneity, spatial heterogeneity) assessments. These measures are outlined below.

2.4.1.1. Species composition

Plant composition was measured using point-intercept frequency measurements (Buttler, 1992). The highest number of contacts of a living plant, with a vertical rod introduced into the vegetation on a point frame, was recorded as the species. Five rods were introduced on the frame and records taken for each; repositioned every 10cm per quarter to record 100 point intercepts per $1m^2$.

Composition data were combined to form plant functional groups (graminoids, forbs, woody plants and other) consistent with the same groupings used for dietary selections in

Chapter 3 (Lamoot et al., 2005). These groups were graminoids - grasses, sedges, rushes; forbs - all herbaceous dicotyledonous species; woody plants; other plants - including mosses, lichens and ferns.

Key species were selected from the composition data, plant species which were commonly present across all habitats or those which represented the habitat (*Agrostis* sp., *Festuca* sp., *Juncus* sp., *Molinia* sp., *Carex* sp., *Calluna* sp., *Erica* sp., *Pteridium* sp. and *Myrica* sp.).

A complete list of all species observed within each subplot was also recorded to eliminate missing or rare species (Buttler, 1992). Plant species that did not intercept the rod, but were still present, were given the minimum value 1 for their occurrence.

2.4.1.2. Sward height

Sward height was measured by the direct measurement of the canopy using a meter rule (Stewart et al., 2001). Measurements were taken eight times from within each sub-plot recording the height of top of the canopy regardless of plant species; a mean canopy height for that sub-plot was calculated.

2.4.1.3. Structural heterogeneity

Structural heterogeneity of vascular plants was assessed using point-intercept frequency measurements (Buttler, 1992). The number of contacts of living plant parts, with a vertical rod introduced into the vegetation on a point frame, was recorded. Five rods were introduced on the frame and records taken for each; repositioned every 10cm for each quarter to take 100 point intercepts per 1m^2.

Buttler's (1992) adapted vertical point method was suited to the array of habitats across the study site, applied to wetland habitat in their work, and adapted from Daget and Poissonets' (1969) point method (Daget and Poissonett, 1969, Buttler, 1992).

2.4.1. 4. Spatial heterogeneity

Absolute and relative plant cover was estimated along with gap, litter, stones, moss and other groupings. Functional group percentage composition was estimated for each subplot for herbs, grasses, legumes and other based on the classifications of Schwab et al.

(2002). The percentage grass and other functional group cover (e.g. gap) were used for assessments of the vegetation heterogeneity.

Vertical heterogeneity in the sward was measured by an estimation of percentage vegetation cover within three height strata (less than 20cm, 20-60cm and above 60cm) within each quadrat. Biomass estimates were also recorded by estimation in the same strata but not analysed, as cover was a suitable comparator. Measures of vertical heterogeneity were utilised in Chapter 4 analyses.

2.5. Statistical Analyses

Among the suite of statistical techniques used in this thesis, analysis of variance (ANOVA) was a prominent approach based on the factorial design of the experimental chapters. Analysis of variance tests the hypothesis that variation in the response variable Y can be partitioned into different levels of one or more explanatory X variable(s). It is an appropriate analysis method for a study with a quantitative outcome (or response variable) and one (or more) categorical explanatory variables. The parametric criteria must be satisfied within the data. The assumptions include that each sample must be approximately normally distributed, the variances of the different samples must be similar (e.g. homogeneity of variances), and observations are independent both within and between samples.

The vegetation measures could be compared between habitats (grassland, heath, mire and woodland) in the analyses of Chapter 4 (herbage removal) and Chapter 5 (trampling) as the parametric analyses allowed this factor to be included. The complexity of the factorial analysis in Chapter 6 (dunging) which assessed the main effects of animal, worming regime and treatment, was too great to include habitat as an additional factor. A four-way analysis of variance would be very difficult to interpret statistically due to the multiple interactions, and is not readily supported by statistical packages (Dytham, 2009).

In the proceeding Chapters 4, 5 and 6, the explanatory variables were treatment, habitat and animal (animal was an addition in Chapter 6 only). The response variables were continuous vegetation parameters. See the respective Chapter statistical analyses sections for further detail.

2.5.1. Frequency-based analyses

The analyses used in Chapter 3 were based on the behavioural frequency-based data and were used to address research objective 1, to quantify and compare herbivore behavioural activity in the heathland landscape and assess the spatial and temporal use through the seasons to determine their influence on the vegetation (*section 1.11*). Details of the specific analyses are outlined in the methods section of Chapter 3.

2.5.2. Species composition

For the impact mechanisms (addressing objective 2 (*section 1.11*)) - herbage removal, trampling and dunging (Chapters 4, 5, 6) - plant species ordinations for treatment and habitat effects were explored using cluster analysis and non-metric multidimensional scaling (NMDS) (Clarke and Warwick, 2001). For the species composition data we used the point-intercept species records on a Bray-Curtis distance matrix (Schiffman et al., 1981, Kohler et al., 2005). All records were included in the data set, including dominant and rarer species. The hierarchical cluster analysis was performed on the Bray-Curtis resemblance matrix after dispersion-weighting transformation, which reduced the effect of dominating species and "noise" (Clarke and Gorley, 2006) and identified the number of groups most supported by the data. A similarity profile test (SIMPROF) provided a means of testing if a specified set of samples or grouping differed from each other (Clarke and Gorley, 2006).

The similarity in the species composition data for the factors habitat and treatment (animal and worming regime for Chapter 6) were detected using NMDS, programme PRIMER v 6.1.13. (Clarke and Warwick, 2001). NMDS was chosen here as it as it allowed flexible comparison of the community assemblages and simple understanding of the sample interrelationships. This approach allowed analysis of the multivariate variation of each dataset.

2.5.3. Architectural vegetation parameters

Parametric analysis was undertaken for the sward height, structural heterogeneity and spatial heterogeneity (addressing objective 2 (*section 1.11*)). Transformations were required for some analyses to meet the assumptions. Please see statistical analyses sections of each chapter for details.

Chapter 3

The spatial and temporal activity of herbivores on the lowland heath system

Summary

Mixed grazing is a viable option for meeting lowland heath conservation objectives. Quantifying herbivore activity assists in understanding comparative foraging, which is particularly important for managing plant communities. In this chapter, three factors were examined in an effort to explain variation in spatial and temporal activity: species (horse and cattle), season (summer and winter) and habitat type (dry heath and wet heath). To understand the differential resource use of the grazers the study asks: (i) does the temporal activity of grazers vary based on species, season and habitat type? And, (ii) are the same factors highly influential in determining spatial patterns of the grazers?

Activity was recorded by observing behaviour, habitat selection, niche breadth and overlap, and spatial occupancy. Feeding and resting distributions were assessed between seasons and habitat types. Habitat selection was estimated and niche breadths were examined for habitat use and diet.

Horses and cattle differed in feeding, which was significantly different on wet heath. Both species' habitat selections were significantly different from availability, particularly for grasslands on both heaths. Habitat use of horses was broader on dry heath, while on wet heath the cattle exhibited this. Dietary overlaps between animals were high, particularly on wet heath.

Temporal variation was primarily due to species differences in digestive physiology and foraging strategy, while seasonal temporal differences were minimal and attributed primarily to forage availability. Variation in spatial activity was due to difference in vegetation composition in each habitat type. Quantifying behaviour and resource-use can inform stocking decisions, like matching availability to control dominating vegetation. The mixed regime demonstrated compensatory and additive effects for habitat type and season. Wet heath can support higher stocking densities due to more quality forage, whilst year-round grazing controlled target vegetation at low stocking densities. Species, season and habitat type are critical in developing a landscape and animal management approach and should be incorporated into a tool to assess grazing management efficacy.

3.1. Introduction

3.1.1. Herbivore activity

The activity of free-ranging herbivores is shaped according to a number of abiotic and biotic factors such as forage availability, foraging strategy and social dynamics (Fleurance et al., 2001, Menard et al., 2002, Lamoot et al., 2005, Kohler et al., 2006b). Three important drivers are also likely to play a central role in influencing observed activity: herbivore species, season and habitat type. The different herbivore species or taxon (i.e. horse and cattle) may be an important determinant of activity because of the differences in physiology and foraging strategy, which often influence temporal and spatial utilisation of habitat (Arnold, 1984, Duncan et al., 1990, Gordon, 2003). Seasonal variation, whilst dictating forage availability, can be influential because of the effect of environmental conditions on activity such as habitat use and feeding patterns (Fehmi et al., 2002, Kohler et al., 2006b). Habitat type is also known to be critical for differential resource use, for instance due to the difference in the vegetation communities between wet and dry habitats, which was strongly associated with seasonal availability (Menard et al., 2002). These factors are also important because of the implications each has on heathland management using grazing herbivores.

3.1.2. Heathland grazing

The unique diversity of habitat and biological communities found in heathlands often grants them their protected designation, typically with specific conservation objectives under European conservation policies. Heathland flora and fauna is dependent on continual habitat management which maintains a sub-climax state of succession (Mitchell et al., 1997). Grazing on lowland heath was a once common and widespread practice, but went through a period of decline before being reinstated to manage these key landscapes (Bullock and Pakeman, 1997, Webb, 1998). The practice can be an effective form of control for invasive and dominating vegetation (Gimingham, 1992) and for maintaining this fragmented and much reduced habitat (Gimingham, 1975).

The traditional approach of maintaining heath and its associated fauna using grazing has been utilised regionally and internationally (Bakker et al., 1983, Newton et al., 2009), and have often employed horses and cattle. It is essential in the process of meeting conservation objectives to understand the comparative activity of these grazers because of the role they play in the functioning system. The animals' differential feeding strategies lead them to forage and consume dominant grasses and woody plants, which are largely the object of management (Menard et al., 2002).

3.1.3. Comparative herbivore grazing

There have been few studies examining comparative spatial and temporal activity of horses and cattle with extensive conservation grazing on British lowland heath, although review documents examining the gap in the knowledge base exist (Bullock and Pakeman, 1997, Lake et al., 2001, Newton et al., 2009). Grazing management has been assessed on systems across continental Europe (Bakker et al., 1983, Bokdam and Gleichman, 2000) and in upland areas of Britain (Grant and Armstrong, 1993, Britton et al., 2005, Fraser et al., 2009) being valuable sources of information. In the New Forest, Dorset, grazing behaviour of ponies and cattle has been studied (Putman, 1986) and the similarities in habitat assemblage and grazing regime with this study were highly relevant. However, Putman's (1986) work made little direct reference to informing modern lowland heath management to meet conservation objectives, but instead approached the problem from an agricultural perspective. Further evaluation is necessary to expand the knowledge of this management practice on lowland heath and to effectively enhance this dwindling habitat and control vegetation in these sensitive systems. In order to understand grazing management and inform decisions for conservation, an understanding of the temporal and spatial aspects of the two herbivores' behaviour is necessary (Grant and Armstrong, 1993, Gordon et al., 2004), which should incorporate the seasonal variation across habitat types.

3.1.4. Functional resource use

Large herbivores utilise their environment by seeking resources by means of optimal foraging and resting primarily (Duncan, 1980, Arnold, 1984, Menard et al., 2002) and by making decisions based on fitness (Laca and Demment, 1996). By seeking quality forage, water and areas to lie up in the animals can meet their key requirements for maintenance, growth and reproduction (Menard et al., 2002). Diet and habitat use have been demonstrated to be integral parts of animal resource use as they spend a majority of their time engaged in foraging behaviour (Illius and Gordon, 1987, van Dierendonck et al., 1996, Menard et al., 2002). However, the use of dietary resources is dependent on seasonal fluctuations and habitat selection for dietary items may be altered if the resources become limited (Lake et al., 2001). Indeed, it is also clear that the intensity of resource use may also increase based on limited availability or indeed prior to periods when availability is limited (Menard et al., 2002).

The functional resource use may be explicitly exhibited on lowland heath systems, where typically species-poor vegetation communities exist and animals move from areas with limited preferred resources to those with higher abundance of lower quality forage (Putman, 1986). Such trends have been shown in sheep and cattle on upland heath where proportions of *Calluna* in the diet increased above grasses from summer to autumn (Grant et al., 1987, Fraser et al., 2009). Patterns of shifting dietary and habitat selection in horses are not widely documented in heathland, due to the lack of documented studies (Putman, 1986, Putman et al., 1987), although these relationships have been documented in the wetlands of the Camargue, where horses moved to preferred habitats with abundant green forage (Duncan, 1983). The work by Putman et al. (1987) showed no correlation between forage availability and habitat use in the New Forest for ponies, which as discussed by Lake et al. (2001), may have been due to other factors like spatial heterogeneity of vegetation (Lake et al., 2001). What is clear is that typically the continual digestive physiology and foraging strategy of horses play some part in selection for forage (Sneddon and Argenzio, 1998, Menard et al., 2002), although the weighting to strategy may be more.

Coexistence of large herbivores on semi-natural systems has been observed through the principal mechanism of resource partitioning (Gordon and Illuis, 1989, Menard et al., 2002, Lamoot et al., 2005). Horses and cattle have been shown to utilise their environment in different ways resulting in niche differentiation despite both being preferential grazers (Pratt et al., 1986). Therefore a direct quantification of niche breath and overlap (diet and habitat), as well as selection of habitat have provided an accurate portrayal of resource use in semi-natural habitats (Menard et al., 2002, Hemani et al., 2004) and have provided comparable measures for behavioural activity studies.

3.1.5. Quantifying spatial and temporal activity

This study quantified the temporal and spatial activity of horses and cattle occupying a lowland heath system during summer and winter seasons within both dry and wet heath habitats, addressing research objective 1 (*section 1.11*). The aim of the study was to quantify the foraging activity of horses and cattle in terms of temporal behaviour, habitat selection and spatial occupancy and niche breadth and overlap (habitat and diet), in order to understand the differential resource use of these grazers.

The work aims to extend our knowledge for informing management on lowland heath systems using grazing regimes and is central to the ongoing management of key lowland heath sites in the United Kingdom (research objective 2 (*section 1.11*)).

Specifically, this chapter seeks to answer the research questions:

(i) Does the temporal activity of grazers vary based on species, season and habitat type?

(ii) Are the same factors (species, season and habitat type) highly influential in determining spatial patterns of the grazers?

3.2. Methods

3.2.1. Study site and animals

Eelmoor Marsh Site of Special Scientific Interest (SSSI) (51.274 N; 0.796 W) is a lowland heath system in north-east Hampshire, UK, (79 ha) supporting over 400 plant and animal species of conservation concern (Hall et al., 2009). Site attributes are available in Chapter 2.

Table 3.1 illustrated the sub-habitat proportions, mapped using a grid system and field survey (Sanderson, 2003) and classified according to dry and wet heath. These two dominant habitat types broadly existed in the system based on the elevations of the north and south of the site, and were appropriate for the landscape assessment of activity. Site characteristics and vegetation communities are described in Chapter 2 (*sections 2.1* and *2.2* of this thesis).

Ten free-ranging Highland cattle (*Bos taurus*) and six Przewalski's horses (*Equus ferus przewalskii*) at stocking densities of 0.25 and 0.18 livestock units per hectare (LU/ha) (dry heath and wet heath, respectively) were employed for the entire study duration. This stocking rate reported differs from Chapter 2, which reported the rates based on the herbivores (0.12 and 0.08 LU/ha for cattle and horses). In this chapter it was appropriate to report this for habitat type as this was the approach for recording activity.

3.2.2. Sampling

Data collected on the dry heath in June to August 2006 for both horses and cattle were from a Master's thesis undertaken by the author. These data were reanalysed for this thesis to incorporate the new comparative assessments across habitat types and season.

The habitat composition was assessed prior to behavioural sampling of the animals using a supervised field survey of and vegetation communities map of the site generated from an NVC survey undertaken in 2003 (Sanderson, 2003) (Figure 2.1).

Table 3.1: Habitat classifications with respective area proportions of Eelmoor Marsh.

Sub-habitat Type	Code	Sub-habitat facets and dominant vegetation	Dry Heath		Wet Heath	
			ha	%	ha	%
Acid grassland	AG	Free-draining, nutrient-poor sandy soils (pH 4-5.5), low species-richness and dominated by fine grasses such as *Festuca* sp., *Agrostis* sp., *Deschampsia* sp. and herbs like *Rumex* sp.	1.3	5.5	0.2	0.4
Neutral grassland	NG	Moderately fertile to nutrient-rich soils (pH ~7), varying in drainage and improvement. Plants include *Lolium* sp., *Festuca* sp., *Anthoxanthum* sp., *Arrhenatherum* sp. and herbs like *Plantago* sp., *Potentilla* sp. *Centurea* sp.	5.2	21.5	6.8	12.4
Molinia mire	MM	Moist to comparatively dry *Molinia*-dominated, which are often oligotrophic mineral soils, and generally moderately acid. Plants include *Molinia* sp., *Myrica* sp., *Calluna* sp. and *Betula* sp. and *Salix* sp.	1.7	7.1	10.8	19.7
Calluna-Heath	H	Dry heath on free-draining soils and humid-heath. Species-poor, dominated by *Calluna* sp., *Erica* sp., *Ulex* sp. on base-poor soil.	5.6	23.3	18.5	33.6
Secondary wood	SW	Semi-natural deciduous or pine plantation. Ground flora dominated by *Rubus* sp., *Pteridium* sp. and *Betula* sp.	1.6	6.5	14.6	26.6
Road verge	RV	Characteristic of approximately neutral soils and plants, slightly improved.	2.9	12.3	2.4	4.4
Other	O	Areas of scrub and dense bracken (*Pteridium* sp.), gorse (*Betula* sp.), or birch (*Betula* sp.) sapling stand.	5.7	23.8	1.6	2.9
Total			24.0	100	54.9	100

Observation of the animals (horse and cattle) in each habitat type (dry and wet heath) and season (summer and winter) were made in separate periods between April 2006 and March 2008. Horse dry summer (June-August 2006), horse dry winter (January-March 2007), cattle dry summer (June-Aug 2006), cattle dry winter (January-March 2007); horse wet summer (July-September 2007), horse wet winter (January-March 2008), cattle wet summer (July-September 2007), cattle wet winter (January-March 2008). For each of these combinations, observation day constituted the replicate, replicated six times. Daytime observations were carried out on one random focal animal between 0600-1800 hours, with twelve separate hours observed for each day and a total of 72 hours per species per season per site. Daytime observations were only undertaken due to sampling constraints, but preliminary observations indicated 24 hour observations were similar to 12 hour observation. The order of observation was scheduled at random, by assigning random values to the scheduled hours, to exclude weather and systematic effects. Pseudo-replication was avoided by random scheduling and by recording herd cohesiveness (i.e. behaviour and distance from conspecifics) to determine independence of activity every 15 minutes (van Dierendonck et al., 1996). Scan-sampling every four minutes over each one-hour duration (Altmann, 1974) recorded behaviour, broad habitat type, dietary selection and spatial occupancy.

An ethogram recorded 25 behavioural codes in an initial preliminary observation period of 60 hours per species. It defined the behaviours as follows:

1	Fe	grazing: eating grasses and herbs, not interrupted by more than 10 seconds of rest, move or other behaviour
2	FeB	browsing: eating woody plants, not interrupted by more than 10 seconds of rest, move or other behaviour
3	ReS	resting standing: standing relaxed, usually rear leg lifted (horse), chewing or ruminating (cattle)
4	ReL	resting lying: lying relaxed, head up
5	Sl	sleeping: lying motionless, lying flat (horse), head down (cattle)
6	W	walk: walking in locomotion, longer than 10 seconds if occurring during grazing
7	R	running: types of locomotion including canter or gallop (horse), run (cattle)
8	Tr	trot: types of locomotion including trot
9	Ch	chase: chasing of other con-specifics or other animal species
10	Vg	vigilance: vigilance on unspecified subject
11	VgO	vigilance on observer
12	VgC	vigilance: vigilance on cattle by conspecific or other animal species
13	VgH	vigilance: vigilance on horse by conspecific or other animal species

14	AlG	allo-grooming: grooming of conspecific
15	AuG	auto-grooming: self-grooming
16	Af	affiliate: sexual or other behaviour
17	Mf	mock-fighting: observed primarily between horses
18	Li	lick: licking of other objects (e.g. mineral licks)
19	Rub	rubbing: rubbing of other objects
20	Fg	fighting: continued severe biting, kicking, vocalisations (primarily horses)
21	Dr	drinking
22	Df	defecation
23	Ur	urination
24	Voc	vocalisation
25	Os	out of site

Following observation and recording of these behaviours, four codes constituted over 85% of activity in both species' (Fe=feeding grazing, FeB= feeding browsing; ReS=resting standing, ReL= resting lying). These were primarily used for assessment of temporal activity, following the methods of van Dierendonck et al. (1996).

Diet was recorded every at each four-minute scan-sample as the forage item selected. Where a plant species could not be instantly identified the broad forage type was recorded (e.g. neutral grass). Weather notes were recorded during the observation periods, and basic weather records were made from the weather station on site.

Spatial occupancy with habitat use was mapped for each species using an alpha-numeric grid square system, devised by the author. Locations were taken at each four minute scan-sample. Each grid square, representing a $50m^2$ area, was assigned a code and overlaid across the entire site. Geodata was attached to each grid square using the geographical information system software, ArcGIS 9 (ESRI Corp.), based on specific habitat classification and behaviour.

3.2.3. Statistical analysis

Frequency distributions were analysed by assessing the proportion of behavioural events observed feeding or resting using a chi-square test (Grafen and Hails, 2008, Dytham, 2009, Hawkins, 2009). These were converted to percentage for graphical representation. The tests examined differences seasonally between dry and wet heath and within and between species. A Spearman correlation analysis tested the relationship of the feeding or resting distributions between seasons and habitat type, after the standardised scores (score/(number of observations) were summed per hour for each animal-habitat-season combination (van Dierendonck et al., 1996).

Based on the proportional habitat use, the data were analysed using Manly's standardised selection index (B_i) which estimated the probability of proportional habitat selection in the *i*th habitat type. The standardised ratios provided selection indices comparable between seasons and animals (Manly et al., 2002):

$$B_i \;= \widehat{w}_i/(\sum_{i=1}^{1} \widehat{w}_j$$

where $\widehat{w}_i = o_i/\pi_i$, the selection ratio,
$o_i = u_i/u_+$, sample proportion of used units,
π_i = proportion of the population of available units that are in category *i,*
u_i = number of units in category *i* in a sample of used units,
u_+ = size of sample of used resource units.

Confidence intervals also indicated departure of selection from the expected, by providing a desired level of confidence.

A log-likelihood statistic (X_L^2) was used to analyse the overall selection values and was appropriate as the proportions of available units in different resource categories were known. It tested if overall selection was proportional to availability (Manly et al., 2002), based on:

$$X_L^2 = 2 \sum u_i \log_e \{u_i / (u_+ \pi_i)\},$$

where u_i is the sample count (proportion habitat used),
π_i is the population proportion (proportion of habitat available).

The niche breadth of habitat use was calculated between species using a standardised index:

$$B_A = B\text{-}1/n\text{-}1,$$

where B is breadth and n is the number of habitat types), derived from Levin's measure of niche breadth ($B = 1/\sum p_i^2$, where p_i is the proportion of selections in habitat i) (Menard et al., 2002, Hemani et al., 2004, Lamoot et al., 2005).

Niche overlap of habitat use was assessed using Pianka's index, an adaptation of MacArthur and Levins' (1967) index appropriate for the habitat types:

$$O_{hc} = \{\Sigma\ (p_{ih} * p_{ic})\}`/\{\ (\Sigma\, p_{ih}^2 * \Sigma\, p_{ic}^2)^{0.5}\}$$

where p_{ih} and p_{ic} are the mean proportional use by horses and cattle, respectively, allocated to the ith resource category (Haering and Fox, 1997, Hemani et al., 2004). This measure ranges between 0.0 when no habitats used are in common, to 1.0 when there is complete overlap in habitat use, providing a suitable analysis for of the interaction between grazers' in terms of habitat use.

For dietary niche breadth the same index was used, where p_i is the frequency of feeding on a particular food type, with chi-square comparisons used to determine significant differences between food type selections. Food types were broadly grouped according to Lamoot et al. (2005): graminoids (grasses, sedges and rushes), forbs (all herbaceous plants), woody plants, and other (mosses, ferns, or unidentified species) (Lamoot et al., 2005). Kulczinski's similarity index (α_{hc}) was applied for dietary overlap between species as it is widely used with the broader food types (Lamoot et al., 2005): $\alpha_{hc} = \sum \min(p_{ih}, p_{ic})$, where p_{ih} and p_{ic} are the proportions of the grazing time that horses and cattle spent foraging on ith food type (Lamoot et al., 2005).

3.3. Results

3.3.1. Temporal differences

Observations of the two major maintenance behaviours, feeding and resting, indicated that temporal activity varied according to habitat type, species and season. These behaviours were examined separately, being mutually exclusive, but were evidently related.

Horses fed for 63-76% of the time and rested for 17-24% (Fig. 3.1) over both habitats and seasons. Figure 3.1 displayed an increase in feeding on dry heath in winter (summer 63.9%, winter 74.8%) but not on the wet heath (summer 76.4%, winter 75.9%), whilst resting showed little variability across seasons and the two heath types. There was no significant difference between season for feeding between dry and wet heath (χ^2 feeding = 0.176, *P*=0.675), the same was true for resting (χ^2 resting = 0.014, *P*=0.905, 1 d.f.).

Feeding and resting in cattle was exhibited in similar proportions (feeding 42-65%; resting 34-49%) from the visual inspection of the frequencies (Fig. 3.1), although in wet heath the cattle did show an elevated feeding activity in winter, 65.1% compared to 53.9% in summer (Fig. 3.1). No significant difference between seasons and feeding was recorded between dry and wet heath (χ^2 feeding = 1.576, *P*=0.209; resting = 2.091, *P*=0.148, 1 d.f.). Variation in temporal activity was not explained by habitat type for horses or cattle (research question (i) for this chapter).

There was no significant difference between species and seasons for feeding or resting on the dry heath (χ^2 feeding=0.848, *P*=0.357; resting=3.073, *P*=0.079, 1 d.f.), although resting approached a level of significance indicating moderate difference between species for resting (*P*>0.05*)*. A significant difference between species and season on the wet heath for feeding was observed, but not for resting (χ^2 feeding = 3.728, *P*=0.050; resting = 0.512, *P*=0.474, 1 d.f.). The research question (i) for temporal variation based on species could not be answered based on this finding. The influence of other factors on this temporal activity is discussed later.

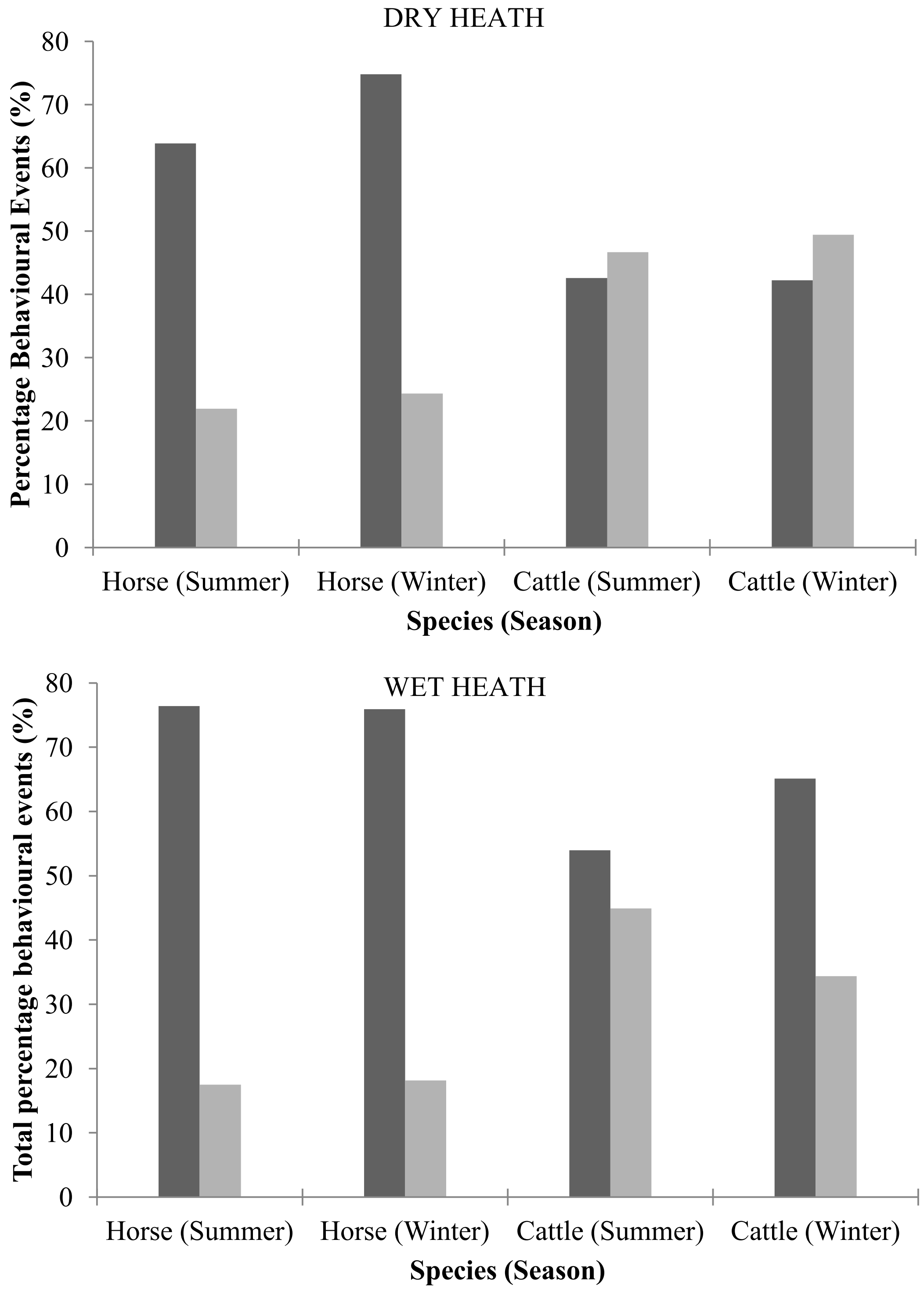
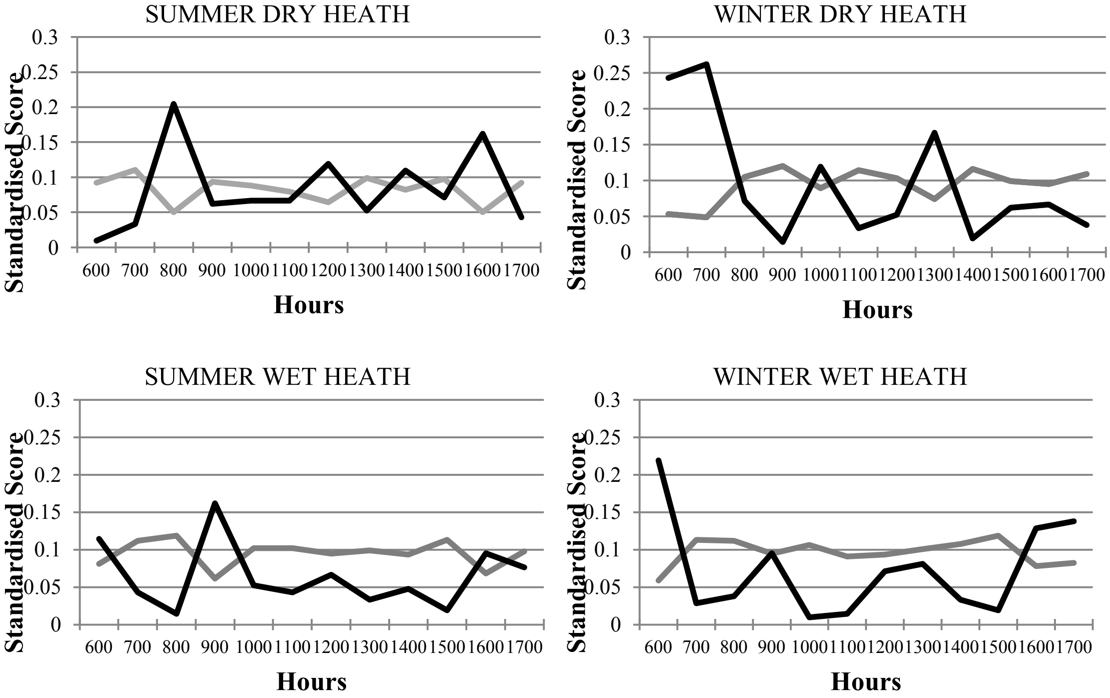


Figure 3.1**:** Total percentage behavioural events for feeding and resting for horses and cattle on dry and wet heath at Eelmoor Marsh. Feeding (dark grey), resting (light grey).

On both the dry and wet heath habitats bimodal patterns of activity were displayed (Fig. 3.2). Horses displayed morning peaks in feeding earlier during winter than summer on both heaths (Fig. 3.2a). Significant correlations between feeding distributions were observed between wet heath winter and wet heath summer (Spearman's r_s: feeding = 0.685, P= 0.014) showing high similarity between these seasons. Resting distributions were dependent on the feeding and therefore were similarly correlated. A significant correlation in feeding between the wet heath summer and dry heath summer for the horses was also noted (r_s: feeding = 0.618, P= 0.032).

The cattle displayed shallower peaks in activity throughout the day, notably in summer with feeding below 0.15 (standardised score) (Fig. 3.2b). Seasonal differences in feeding were similar to the patterns observed in the horses, i.e. bimodal peaks in winter at 06:00-07:00h and 13:00-15:00h. Resting was mirrored. For cattle, a significant correlation was observed for feeding between wet heath winter and wet heath summer (r_s: feeding = 0.616, P= 0.033), indicating similarity between seasons for wet heath.

(a) HORSE



(b) CATTLE

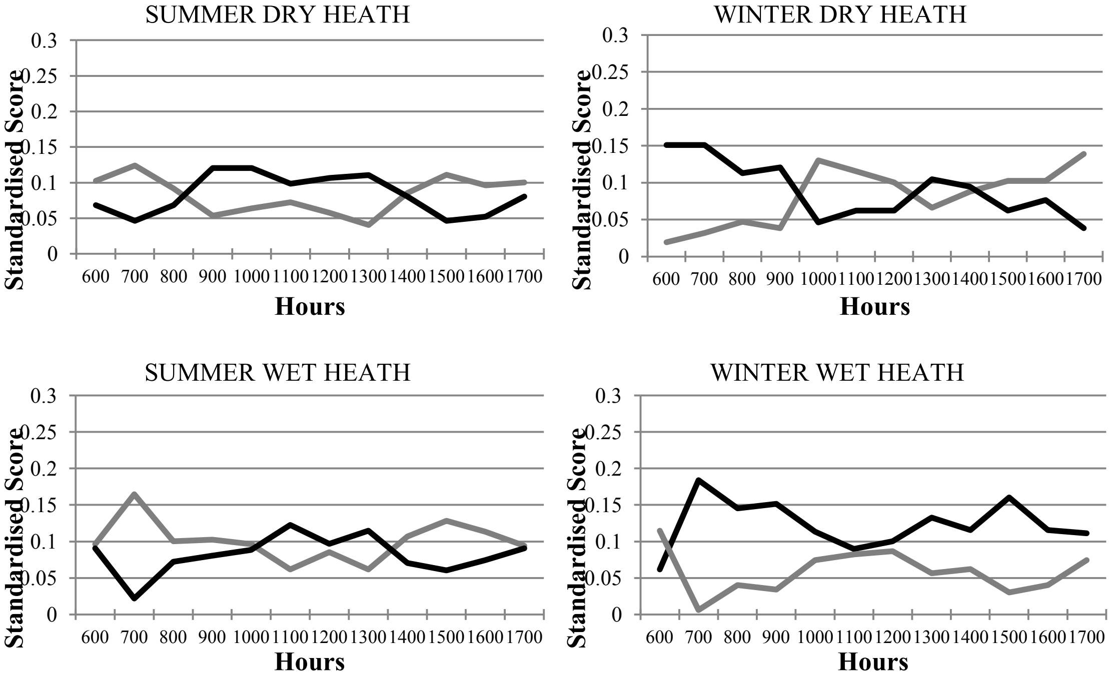


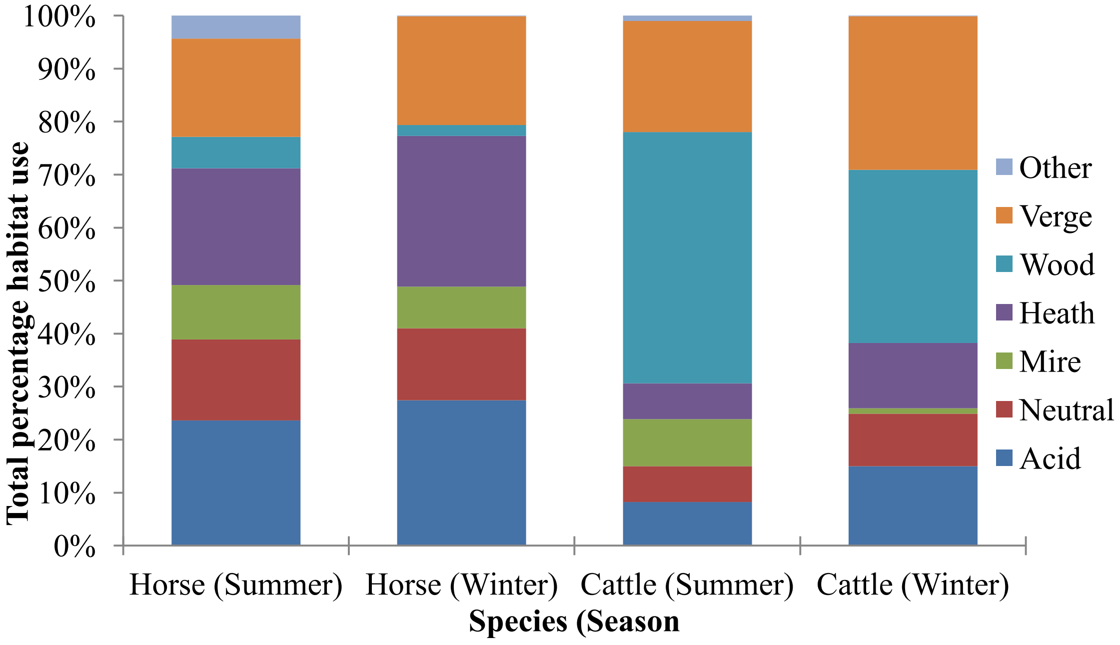
Figure 3.2**:** Horse (a) and cattle (b) feeding and resting distributions throughout the daytime period within dry and wet heath habitats and seasons. Feeding (BLACK line), resting (GREY line). Proportional feeding and resting distributions converted to a standardised score.

3.3.2. Habitat selection

The grazers displayed similarities in habitat use between the dry and wet heath systems, (Fig. 3.3). Within the dry heath, horses occupied acid grassland, despite its reduced availability (Table 3.1), heath and road verge (three sub-habitats collectively summer 64%; winter 76%). The cattle utilised secondary woodland and road verge differently between seasons (woodland: summer 47%; winter 32%; road verge: summer: 21%, winter: 29%) (Fig. 3.3).

On the wet heath each grazer showed differences across seasons. Horses increased use of neutral grassland (summer: 42%, winter: 49%), while this was reduced on road verge in winter. Cattle also utilised neutral grassland extensively in winter (summer: 25%, winter: 42%), a sub-habitat that constituted 12% cover compared to acid grassland cover (0.4%). Secondary woodland was occupied for 27% of the time in summer but only 5% in winter by cattle.

(a) DRY HEATH



(b) WET HEATH

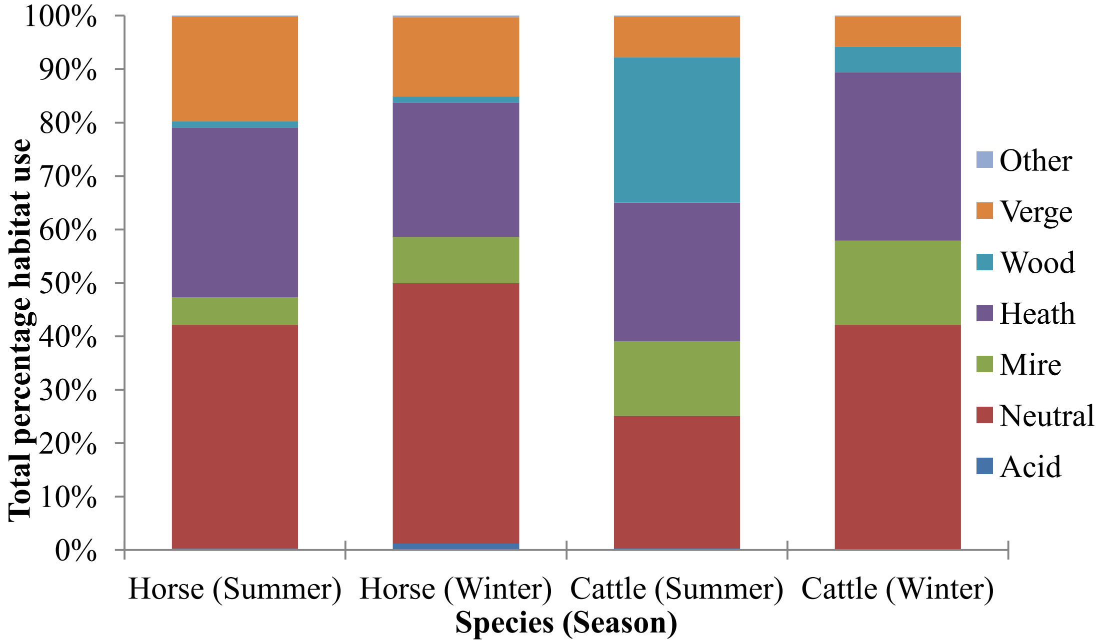


Figure 3.3: Total percentage habitat use for horse and cattle within summer and winter on (a) Dry heath and (b) Wet heath habitats.

The standardised selection indices (Table 3.2) provided an estimate of the probability of selecting the *i*th sub-habitat. On dry heath horses displayed a marked selection for acid grassland (summer B_1=0.427; winter B_1=0.500), and less for neutral grassland (summer B_2=0.071, winter B_2=0.064), despite the availabilities (i.e. population proportions) (Table 3.2 and Table 3.1). The cattle selected acid grassland and road verges (summer: B_1=0.119, B_6=0.138; winter: B_1=0.240, B_6=0.211) but selected secondary woodland primarily (summer: B_5=0.591; winter: B_5=0.449).

The selection on wet heath by horses for acid grassland (summer: B_1=0.071; winter: B_1=0.259) was not observed in cattle (summer B_1=0.128, winter B_1=0.034). Neutral grassland was selected by horses equally across seasons (summer B_2=0.343; winter B_2=0.338) but disproportionately by cattle (summer B_2=0.276; winter B_2=0.493). The selection for road verge was high on wet heath despite its low availability (Table 3.2) in horses (summer B_6=0.452; winter: B_6=0.289) but not in cattle (summer B_6=0.239; winter: B_6=0.190). Selection by cattle for secondary woodland in dry heath was higher than wet heath, and differed seasonally on wet heath (summer B_5=0.142; winter: B_5=0.026).

Log-likelihood statistics (X_L^2) (Table 3.3) were all highly significant ($P<0.01$, 6 d.f.) when compared to the chi-squared distribution, indicating that overall there was a marked departure from the expected that habitat use is random and proportional to availability. There was therefore evidence to answer research question (ii) that habitat type was critical in explaining variation in spatial activity.

Table 3.2: Habitat use sample proportions with accompanying confidence intervals and selection indices for each animal species on (a) dry heath and (b) wet heath. AG: acid grassland, NG: neutral grassland, MM: *Molinia* mire, H: heath, SW: secondary woodland, RV: road verge, O: other.

(a) DRY HEATH SUMMER

Habitat	**Used sample (o_i) ± CI**		**Population Propn. (π)**	**Standardised Index (B)**	
	Horses	Cattle		Horses	Cattle
AG	0.236 ± 0.003	0.082 ± 0.006	0.055	0.427	0.119
NG	0.153 ± 0.004	0.068 ± 0.007	0.216	0.071	0.025
MM	0.103 ± 0.005	0.089 ± 0.006	0.071	0.144	0.100
H	0.220 ± 0.003	0.068 ± 0.007	0.234	0.094	0.023
SW	0.059 ± 0.007	0.474 ± 0.001	0.064	0.092	0.591
RV	0.185 ± 0.003	0.209 ± 0.003	0.121	0.153	0.138
O	0.044 ± 0.008	0.010 ± 0.018	0.239	0.018	0.003
	1.000	1.000	1.000	1.000	1.000

DRY HEATH WINTER

Habitat	**Used sample (o_i) ± CI**		**Population Propn. (π)**	**Standardised Index (B)**	
	Horses	Cattle		Horses	Cattle
AG	0.274 ± 0.003	0.150 ± 0.004	0.055	0.500	0.240
NG	0.136 ± 0.004	0.099 ± 0.005	0.216	0.064	0.041
MM	0.079 ± 0.006	0.010 ± 0.018	0.071	0.111	0.013
H	0.284 ± 0.002	0.123 ± 0.005	0.234	0.123	0.047
SW	0.020 ± 0.0012	0.327 ± 0.002	0.064	0.032	0.449
RV	0.206 ± 0.003	0.290 ± 0.002	0.121	0.171	0.211
O	0.001 ± 0.060	0.001 ± 0.060	0.239	0.000	0.000
	1.000	1.000	1.000	1.000	1.000

(b) WET HEATH SUMMER

Habitat	**Used sample (o_i) ± CI**		**Population Propn. (π)**	**Standardised Index (B)**	
	Horses	Cattle		Horses	Cattle
AG	0.003 ± 0.034	0.004 ± 0.030	0.004	0.071	0.128
NG	0.419 ± 0.002	0.247 ± 0.003	0.124	0.343	0.276
MM	0.052 ± 0.008	0.140 ± 0.004	0.197	0.027	0.098
H	0.318 ± 0.002	0.259 ± 0.003	0.336	0.096	0.107
SW	0.012 ± 0.016	0.272 ± 0.003	0.266	0.005	0.142
RV	0.195 ± 0.003	0.076 ± 0.006	0.044	0.452	0.239
O	0.002 ± 0.042	0.002 ± 0.042	0.029	0.006	0.009
	1.000	1.000	1.000	1.000	1.000

WET HEATH WINTER

Habitat	**Used sample (o_i) ± CI**		**Population Propn. (π)**	**Standardised Index (B)**	
	Horses	Cattle		Horses	Cattle
AG	0.012 ± 0.016	0.001 ± 0.060	0.004	0.259	0.034
NG	0.487 ± 0.001	0.420 ± 0.002	0.124	0.338	0.493
MM	0.087 ± 0.006	0.157 ± 0.004	0.197	0.038	0.116
H	0.251 ± 0.003	0.316 ± 0.002	0.336	0.064	0.137
SW	0.012 ± 0.016	0.047 ± 0.008	0.266	0.004	0.026
RV	0.148 ± 0.004	0.057 ± 0.007	0.044	0.289	0.190
O	0.003 ± 0.034	0.001 ± 0.060	0.029	0.008	0.005
	1.000	1.000	1.000	1.000	1.000

Table 3.3: Log-likelihood statistics (X_L^2) for horses and cattle on each habitat type across summer and winter. 6 d.f. Significant at P=0.01

	Dry heath		Wet heath	
	Summer	Winter	Summer	Winter
Horses	679.64	1122.98	1446.91	1449.96
Cattle	1988.19	1627.84	211.16	836.68

3.3.3. Niche breadth and overlap

Horses displayed a higher breadth in both seasons on the dry heath (B_A summer 0.63, winter 0.57), than cattle (B_A summer 0.39, winter 0.53). On the wet heath the horses displayed similar niche breadths across seasons (B_A summer 0.36, winter 0.34), whilst the cattle had niche breadths of 0.57 in the summer, and 0.38 in the winter.

Habitat use overlap (Pianka's index) between the grazers indicated a much lower overlap of habitat use on the dry heath (O_{hc} dry heath summer 0.53, winter 0.68) with considerably higher indices on the wet heath (O_{hc} wet heath summer 0.79, winter 0.96).

3.3.4. Spatial occupancy

Occupancy was highest in the grassland areas for horses and on road verge edges, with moderate occupancy in heath (Fig. 3.4a). The higher occupied areas (darker shade) in the south and east of the site represented the low-lying grassland habitats, while the occupancy in the centre-north of the site was largely heathland habitat (Appendix 2). The cattle utilised the woodland areas intensively indicated by the darker shade in north-centre and west centre (Fig. 3.4b). Cattle occupied the site more extensively than horses (Fig 3.4b), supported by the habitat selection indices (Table 3.2), but approximately equal occupancy in the south and east grass-dominated habitats. Moderate occupancy was observed in the heath areas (the north-east of the site), at a similar extent to horses (Fig. 3.4).

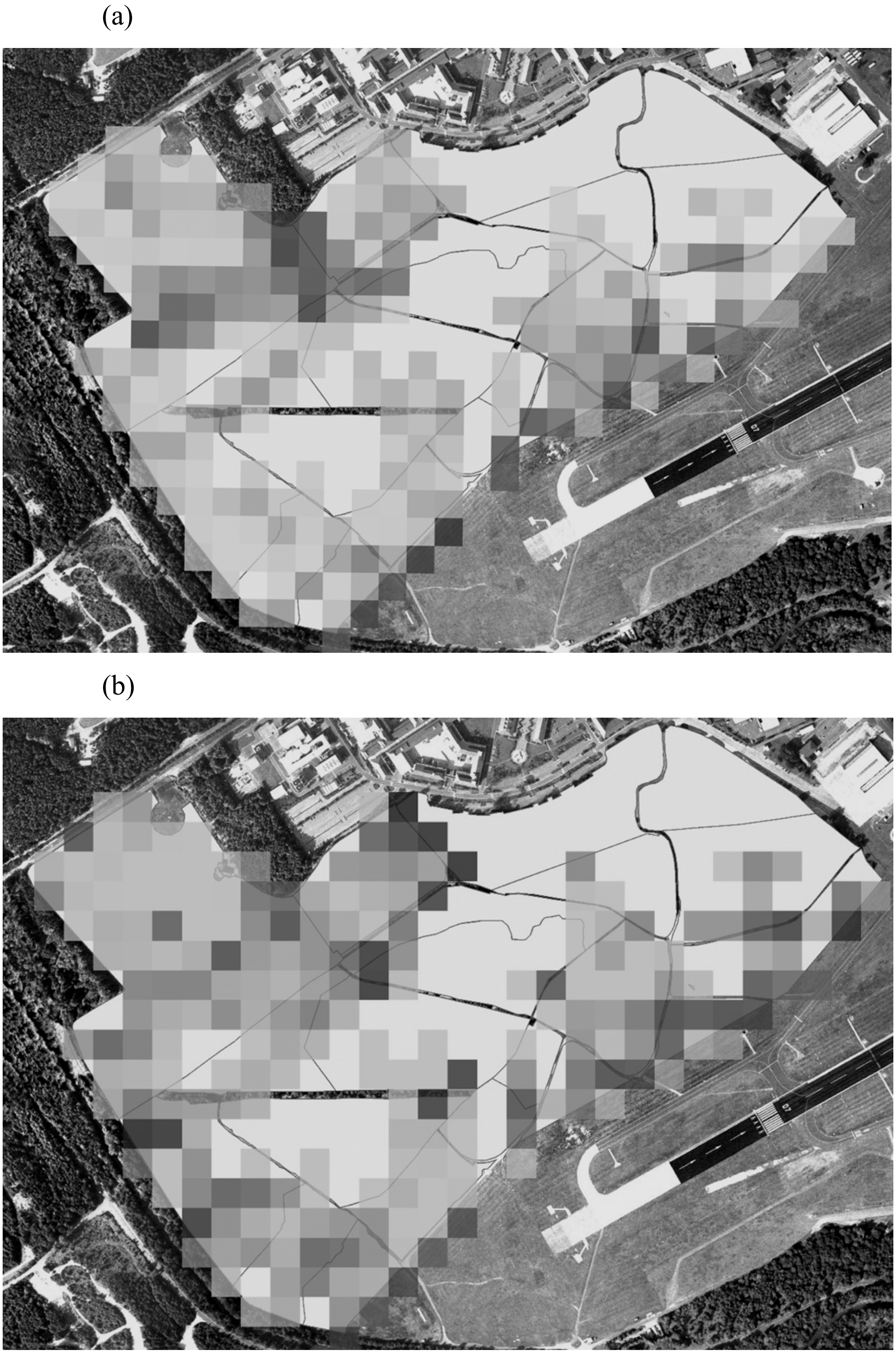


Figure 3.4: GIS raster images of horse and cattle occupancy data across Eelmoor Marsh. (a) Horse occupancy (greyscale gradient of use: 0-179 scan samples) (b) Cattle occupancy (greyscale gradient of use: 0-212 scan samples). © Copyright Getmapping 2012.

3.3.5. Dietary preference

Both grazers foraged predominantly on the graminoids across all seasons and sites (Table 3.4 and 3.5). Cattle were observed to forage on woody plants such as *Rubus* sp., *Calluna* sp., *Ulex* sp. and *Betula* sp. The horses did select woody plants, but to a much lesser extent than the cattle, e.g. *Ulex* sp. and *Salix* sp., and only on the dry heath despite its availability on the wet heath. The chi-square statistic for grouped diets displayed a highly significant departure from the expected for equal use (Table 3.4).

Table 3.4: Proportional selection of dietary groups across dry and wet heath habitats and summer and winter, with calculated niche breadths and chi-squared statistics (all significant at $P<0.01$, 3 d.f.).

	Dry heath summer		Dry heath winter		Wet heath summer		Wet heath winter	
Habitat	Horses	Cattle	Horses	Cattle	Horses	Cattle	Horses	Cattle
Graminoids	0.98	0.77	0.97	0.87	1.00	0.95	0.99	0.92
Forbs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Woody plants	0.02	0.23	0.02	0.08	0.00	0.05	0.01	0.08
Other	0.00	0.00	0.02	0.05	0.00	0.00	0.00	0.00
Total	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**
Niche breadth	0.007	0.092	0.011	0.053	0.001	0.016	0.004	0.030
χ^2	1711.6	584.9	1920.2	697.6	1845.1	1201.1	1866.6	1473.9

The calculated niche breadths for grouped diets indicated that both species had a minimal dietary width across habitats and seasons. Horses had a limited dietary range because of their high proportional use of graminoids while cattle exhibited a marginally broader range because of woody plants selection (Table 3.4). Dietary niche overlap between grazers indicated that a greater overlap existed in winter than in summer on dry heath (O_{hc} dry heath summer 0.96, winter 0.99), with both seasons on wet heath indicating high overlap (wet heath summer 0.99, winter 0.99).

Both grazers foraged on neutral grass at the same proportion in all habitats and seasons (Table 3.5). The dietary selections indicated that horses and cattle did select some plant species more extensively than others, such as the high selection for *Rubus* sp. and *Betula* sp. by cattle across all habitats and seasons. *Molinia caerulea* was selected more on wet heath than dry heath by cattle. Kulczinski’s index indicated that there was high similarity between grazers for willow (*Salix* sp.*)* in the dry heath winter ($\alpha_{\text{hc}} = 0.13$), and in the wet heath summer ($\alpha_{hc} = 0.09$) and winter ($\alpha_{hc} = 0.09$). This was evident for *Molinia caerulea* on dry heath summer ($\alpha_{hc} = 0.41$), and on the wet heath, but to a lesser extent (Table 3.5).

Table 3.5**:** Species dietary selections across dry and wet heath habitats and summer and winter with accompanying Kulczinski's similarity indices. H=horse; C=cattle (Grouped compositions see Table 3.1)

Dietary selection	DRY HEATH SUMMER			DRY HEATH WINTER			WET HEATH SUMMER			WET HEATH WINTER		
	H	C	Index	H	C	Index	H	C	Index	H	C	Index
Acid grass	221	44	0.44	404	139	0.74	0	0	0.00	12	0	0.00
Neutral grass	417	255	0.62	274	195	0.58	628	296	0.68	624	350	0.64
Molinia caerulea	47	67	0.41	1	9	0.09	31	142	0.18	28	139	0.17
Rubus sp.	3	36	0.08	0	26	0.00	0	3	0.00	0	9	0.00
Ulex europaeus	6	8	0.08	4	0	0.00	0	0	0.00	1	16	0.06
Cirsium sp.	1	2	0.02	0	0	0.00	0	0	0.00	0	0	0.00
Betula pendula	0	30	0.00	7	0	0.00	0	9	0.00	0	9	0.00
Crataegus monogyma	0	2	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Rumex sp.	0	2	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Quercus sp.	0	1	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Salix sp.	3	13	0.13	0	6	0.00	3	9	0.09	8	9	0.09
Calluna vulgaris	0	1	0.00	11	21	0.21	0	0	0.00	0	0	0.00
Lonicera periclymenum	0	1	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Juncus sp.	3	5	0.05	0	0	0.00	0	0	0.00	1	0	0.00
Carex sp.	4	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Total	706	467		761	427		823	602		835	634	

3.4. Discussion

On lowland heath, species, season and habitat type did explain much of the variation in temporal and spatial trends, and the quantification of activity and resource use provided valuable knowledge for using grazers to manage vegetation.

3.4.1 Variation by species

The grazers utilised their environment in very different ways. The horses spent longer periods feeding during their day and rested for only a small proportion (Fig. 3.1), indicative of their digestive physiology and continual foraging strategy (Sneddon and Argenzio, 1998). The balanced feeding and resting observed in cattle (Fig. 3.1) is characteristic of their less intensive foraging (Arnold, 1984) , supported by a statistically-significant difference between the grazers for seasonal feeding on wet heath. Species differences were large on the dry heath and wet heath, but the superior habitat availability and foraging opportunities on the wet heath are likely to have been exploited by horses, resulting in the disparity (Fig. 3.1). Research question (i), whether temporal activity varied based on species, could not be answered based on the proportional feeding and resting.

The elevated feeding scores and repeated peaks (Fig. 3.2) described the high rate of foraging and efficient throughput of the equid physiology (Sneddon and Argenzio, 1998). Ruminants, contrastingly, retain fodder for maximal digestion (Menard et al., 2002), which resulted in a slower overall forage rate and feeding score with longer resting durations (Fig. 3.2). The cattle were driven to forage for longer, especially in winter when forage availability was lower, as supported by the higher feeding time and differential habitat use (Figs. 3.1 and 3.2). The fact that no correlations were displayed between species for the feeding distributions supported research question (i) for species. The exception for wet winter feeding was probably due to the crepuscular feeding recorded for both species, observed particularly in horses (Scheibe et al., 1998, Berger et al., 1999).

The species differences in temporal activity, addressing research question (i), observed in wet heath was indicative of the vegetation composition of a more productive habitat with higher availability of green forage (Menard et al., 2002). The limited availability of quality habitat on the dry heath would have suggested a high overlap between species, which was only moderate (i.e. Pianka's index), suggesting that competitive exclusion did occur, as observed by Putman (1996) in similar systems (Putman, 1996).

The benefit of conservation grazing is driven largely through the differential spatial selection of foraging habitat, the animals' habitat use being linked with their feeding and resting activity (Lamoot et al., 2005). The horses used grassland which suits their digestion and incisor morphology and crop short swards rapidly (Menard et al., 2002), which is beneficial for maintaining a diverse sward mosaic (Bullock and Pakeman, 1997). The high occupancy of these habitats by horses (Fig. 3.4) supported the high feeding reported (Fig. 3.1) as well as the feeding distributions (Fig. 3.2) which indicated long foraging periods. The occupancy is also likely to have supported the habitat selection indices (Table 3.2) for these grass-dominated habitats. The cattle displayed narrower habitat use breadths (i.e. Levin's index) on dry heath due to a high selection for secondary woodland (Table. 3.2) and woodier plants of medium nutritional value (Table 3.4) which they are able to digest (Menard et al., 2002). On the wet heath the cattle had wider habitat and dietary niche breadths than the horses, switching to heath and neutral grassland accompanied by a broader diet, (Table 3.2 and 3.4) because of the comparative size of wet heath and increased forage availability. The cattle had a highly selective feeding strategy but from a wider dietary range (Table 3.5). Because of their inability to utilise shorter swards because of their incisor morphology (Krysl et al., 1984, Hongo and Akimoto, 2003) the species complemented one another's spatial activity. This compensatory spatial activity is of high value for conservation management (Menard et al., 2002)and meant research question (ii) was answered that the variation in spatial activity was explained by species.

The high habitat use overlap (i.e. Pianka's index) and occupancy in wet heath between the grazers (Table 3.2 and Fig. 3.4) contrasts with the separation of spatial activity, showing a mutual selection for resource-rich neutral grassland and road verge habitats. However these were likely to occur at different times as there was potential for strong competition and exclusion, as seen in the temporal activity. It is documented that these grazers influence and overlap one another's habitat use, displayed through exclusion and competition (Gordon and Illuis, 1989, Putman, 1996) and Menard et al. (2002) concluded that equids and bovids displayed a resource-partitioning strategy to explain co-existence with differing diets (Menard et al., 2002). The low overlap of dietary selections in most of the plant species supported this strategy (Table 3.5), which has been documented in moorland and other habitats (Gordon and Illuis, 1989, Sietses et al., 2009). As resource-partitioning provides an answer for the overlap, the remaining findings provide sufficient evidence to answer research question (ii), and species explained variation in spatial activity.

3.4.2. Seasonal effects

Seasonal variability in activity is often brought about by environmental factors such as weather, but also associated factors like forage availability and vegetation nutritional value (Duncan, 1983, Fleurance et al., 2001, Gander et al., 2003). Seasonal trends are useful for estimating habitat utilisation, although this factor is variable and difficult to predict for year-to year management, which is important to understand for managing a sensitive habitat such as heathland (Grant and Armstrong, 1993). In this study, horses fed earlier and at a higher rate in winter on the dry heath (Fig. 3.2a), when forage was less available and energy requirements were high (Begon et al., 1996). This matched the seasonal shift in feeding time observed in Camargue horses (Menard et al., 2002). This pattern was not seen in the wet heath where feeding was maintained at the same level and a correlation was observed between seasons. It was possible the smaller size of the dry heath and limited availability of foraging habitats meant seasonal variation effects were more apparent than on the wet heath.

Increased feeding and a marginally higher feeding rate were observed in the cattle in winter on the wet heath (Figs. 3.1 and 3.2b). These differences may have been attributed to increased forage availability or elongated feeding bouts in summer, when they could take advantage of increased daylight associated with easier predator avoidance behaviour (Hodgson and Illius, 1996). However, a significant correlation, like that seen in horses on wet heath between seasons, showed that the cattle did not change their feeding or resting due to season and so little evidence to answer this part of research question (i) which asked if temporal activity was explained by season. The nutritional value of vegetation may have been important for determining activity (Fleurance et al., 2001, Gander et al., 2003) as the evidence here suggested that the horses were able to compensate for low quality forage on the dry heath by increasing the proportion and rates of feeding

(Gudmundsson and Dyrmundsson, 1994), whereas the cattle were only able to do this on wet heath where more nutritious plants were widely available (Menard et al., 2002). More work is required.

The horses showed a high tolerance for seasonal extremes in spatial activity as documented in a number of studies (Pereladova et al., 1999, Linklater et al., 2000) displaying typical equid characteristics, feeding continually on localised habitats with a high selection for grasslands irrespective of season (Fig. 3.3 and Table 3.2) (Pratt et al., 1986, Fleurance et al., 2001, Lamoot et al., 2005). This spatial activity may have been due to the strict adaptation for monocotyledon species (Sneddon and Argenzio, 1998), i.e. narrow dietary breadths (Table 3.4), but the primary reason was likely to be associated with the abundance of highly palatable and nutritious graminoids (Cran et al., 1997). This trait is likely to be advantageous for managers using horses to target dominant vegetation such as *Molinia caerulea* (Table 3.5). Cattle, however, sought refuge (i.e. secondary woodland) for longer periods in summer (Fig. 3.3 and Table 3.2) but selected a wider breadth of plants (Table 3.4) for maximal digestion in winter when high-quality forage diminished (Lamoot et al., 2005, Kohler et al., 2006b). This was also supported by increased selection for neutral grassland and road verge in winter, driven by their energy requirements (Olson and Wallander, 2002).

The differential seasonal findings only provided some explanation for the spatial activity and specific weather conditions, e.g. wind or temperature, may be contributing (Duncan, 1980). Based on the findings of this study, season did not offer adequate evidence to account for the variation in activity, and so both the temporal and spatial research questions (i and ii) cannot be answered based on season. The temperate climate of the study site may have explained the minimal difference between seasons, particularly given the contrasting evidence in other geographical regions (Menard et al., 2002, Morel et al., 2006), so regional environmental conditions should be accounted for in grazing management. Season is highly variable, and unlike vegetation composition which is likely to be important for making grazing management decisions, cannot be influenced through the management of a site. The findings indicated that the effect of species and habitat type were much more influential on the temporal activity than season.

3.4.3. Dry and wet heath habitat

Some of the same factors discussed previously, forage and habitat availability, contributed to the variation between dry and wet heath. The significant temporal differences observed between the heaths for cattle feeding was likely to be caused by respective sub-habitat composition, but seasonal availability may have had an additive effect. The feeding and resting distributions showed no correlation between the two types of heath, except for horse summer feeding which could be caused by the rigid feeding patterns of horses (Fig. 3.2). It was apparent from the temporal activity that habitat type may have offered some explanation for the observed variation, so quantifying these vegetation communities would make stocking decisions and controlling vegetation clearer for the manager in these habitats, although herbivore species differences are key.

Within each habitat, factors such as palatability and quality of forage were likely to be as important to spatial activity as the vegetation composition (Bokdam and Wallis de Vries, 1992, Hodgson and Illius, 1996, Hester and Baillie, 1998), as demonstrated by the selection of scarcely-available acid grassland on dry heath. Increased soil fertility from surface run-off to road verges which enhanced botanical richness may have attributed for the high selection on dry heath, which only constituted less than two per cent of the area (Table 3.2a). It is these factors that were important for determining differential resource use, illustrated in mixed grazing regimes in French wetlands balancing quality and quantity of available green forage (Bonis et al., 2005). While availability was likely to be highly influential, vegetation composition remained critical in determining spatial activity, e.g. cattle selected *Betula* sp. on dry heath when suitable grass species were limited (Table 3.5). Competitive exclusion must not be ruled out based on the literature (Menard et al., 2002, Hemani et al., 2004) and the findings (i.e. Pianka’s index) of habitat use overlap. The findings answered the habitat component of research question (ii) posing the question if habitat type influenced spatial activity.

In terms of limitations of the study, the sampling method meant there were concerns over pseudo-replication of dominant and leading animals in the groups. This was accounted for by random allocation of the sampling hours per animal and a measure of herd cohesiveness to ensure independence of activity from conspecifics, as utilised in other activity studies (van Dierendonck et al., 1996). This is a constraint of field observation of semi-wild ungulates, as is the frequency-based data derived from such behaviour-based studies which meant only non-parametric assessments could be made.

3.4.4. Implications for lowland heath management

The commonly adopted mixed grazing regime can offer an opportunity to meet broad conservation objectives, restoring important components of the ecosystem at the appropriate density in fragmented and declining heath systems (Grant and Armstrong, 1993, Bullock and Pakeman, 1997). Species, season and habitat type were valuable explanatory variables that have not been previously examined on lowland heath for understanding the trends in temporal and spatial ecology of grazers. Although season was less informative about changes in activity, which may be due to reasons such as regional climatic conditions, season and habitat together have been shown to be influential. These variables affect grazing activity because different habitat types are composed of different plants and these have varying chemical compositions, which is influenced by season (Fraser et al., 2009). By understanding plant-animal interactions, the knowledge provided here can now be used as a management tool by selecting the appropriate animal species or mix to manage the vegetation. For instance, horses should be employed for directly targeting graminaceous plants such as *Molinia* sp. and others.

Lowland heath is a unique and specialist habitat of international importance. Broadening the available knowledge for meeting conservation objectives with mixed grazing is necessary both on economic and ecological grounds and has not been accomplished on a study site that can exclude external factors (e.g. grazing from other wildlife). Employing mixed grazing regimes on lowland heath generate additive and compensatory effects for targeting graminaceous vegetation because of their differential foraging strategies and resource use across habitat types and season. This is beneficial for the longevity of protected reserves. Other regimes which incorporate animals that persistently browse as well as graze (e.g. goats) (Lake et al., 2001) are likely to be suitable for addressing the minimal woody plant and forb selection observed in this study (Table 3.4), an ongoing problem on lowland heath (Manning et al., 2004).

The work has shown that wet heath could support a higher level of stocking with minimal overlap due to a more diverse habitat composition (Table 3.2) and available quality forage. Many heathland sites also employ seasonal grazing only through the summer months, targeting the vegetation when growth is at its most vigorous and minimising the damage to heather, but the year-round grazing at the low-stocking level adopted here has shown a switching behaviour in foraging strategy and diet. Therefore, based on this study, low-density mixed regime should be adopted for meeting conservation targets such as controlling dominating graminoids. The factors collectively have value for understanding activity because they are present across all lowland heath systems and can be easily-assessed and incorporated early on in the decision-making process.

In summary, the specific recommendations based on this regime and study site are:

- Horses, in particular, should be used to target graminaceous plants, including purple moor grass (*Molinia caerulea*), but cattle should also be adopted for this aim;
- Managers should employ horses and cattle together as they generate additive and compensatory effects on the vegetation, across habitat types and seasons;
- Employing other animal species/breeds may be advised to browse the woody plants mostly avoided by the grazing regime in this study;
- A stocking density of 0.18-0.25LU/ha can be employed on systems with mixed heath habitats to achieve a heterogeneous spatial and temporal use of the system;
- Year-round low-density mixed grazing regimes are recommended to target dominating vegetation, based on this study, as the animals show a switching behaviour in foraging.

Quantifying activity was essential for understanding the comparative foraging of mixed grazing regimes, and the chapter has met research objective 1 of the thesis. The study is valuable for optimising stocking levels and for the control of dominant and invasive vegetation. The work has provided a basis for examining the grazers' ecological impact on floral and faunal communities which can be used as a tool to understand the vulnerable nature of heath and to manage vegetation communities effectively.

In this study, linking these landscape scale effects in this chapter to the micro-scale vegetation impacts, reported next in this thesis, is valuable for understanding and quantifying the multiple factors responsible for governing vegetation communities. In the following three data chapters the ecological impacts of the herbivores are experimentally assessed, examining the biological and architectural effects on vegetation communities.

Chapter 4

The impacts of herbage removal on lowland heath vegetation

Summary

Herbage removal alters plant community composition and its architecture and herbivore regimes are widely-adopted in semi-natural habitats. Lowland heath has suffered declines in the last century and a lack of experimental study is evident for informing managers. This study took a novel approach to quantifying the separate and actual impacts of herbivore grazing to inform decisions, rather than making simulated estimations of this impact as documented in the literature. The chapter asked if herbage removal modified plant species composition, whether low-density grazing altered sward height and if structure and cover were enhanced by the same grazing across the habitats.

Mixed (horse and cattle) low-density grazing was evaluated across grassland, heath, mire, woodland. Changes to species composition, sward height, structural heterogeneity and spatial cover were assessed and analysed with two-way analysis of variance (treatment×habitat). Non-metric multidimensional scaling (MDS) examined the similarity between plant compositions. Plant species diversity between the main effects was tested using analysis of covariance accounting for Foliage Height Diversity (FHD).

Plant community effects were not clearly defined and only graminoids displayed significant differences, although some key plant species had significant interactions (*Molinia* and *Carex*). Herbage removal strongly governed architecture (sward height, structure, spatial heterogeneity (gap cover)). There was no significant difference in plant species diversity for herbage removal with FHD.

The low-density mixed regime, governed architecture especially in graminoid-dominated habitats, but modifications to plant community were not as clear, although the findings were of benefit for lowland systems where control of grasses is a priority. Structural declines were due to reduced vegetation height and density at the micro-scale but this may not be true at the patch-level, further work is needed. Increases in gap cover are likely to provide colonisation sites for less competitive plants, although grass cover displayed capacity for lateral growth. The control of invasive grasses and creation of spatially heterogeneous vegetation was beneficial for making management recommendations.

4. 1 Introduction

4.1.1. Large herbivore foraging

Large grazing herbivores modify their surrounding vegetation through differential selection of forage or food items, removing or damaging plant biomass and directly altering plant and habitat structure (van Andel, 1999). A grazing animal moving through the vegetation selects plants according to a number of biotic and abiotic factors, removing plants or plant parts as they come into their grazing horizon (Lemaire and Chapman, 1996). These selections are often from patches that they have previously selected from (Ungar, 1996) and are likely to be key species or select dietary items. These selections govern vegetation parameters, which in turn influences forage availability. The relationship between intake rate and abundance of forage, or the functional response, constrains an animal's foraging behaviour as it reaches an asymptote and the rate of intake reaches a maximum (Ungar, 1996) and consequently it constrains the impact of grazing on vegetation.

The plant community and architectural changes to vegetation between grazed and ungrazed areas have been documented for a number heath systems (Newton et al., 2009). The changes are highly dependent on the habitat type, seasonal availability of vegetation and grazing regime, (see chapter 3) as well as the duration of herbage removal (Kohler et al., 2004). Selective feeding from grazers generates a natural vegetation mosaic where there is a mix of plants with different tolerances to grazing (Oom et al., 2008). For example, areas avoided by grazers (usually because the vegetation in that area is not of high quality or its chemical constituents) become taller and older compared with areas that are more heavily grazed. At the microhabitat scale the canopy structure and cover is altered by grazing, modifying the micro-climate, which has implications for colonising plants. The vegetation mosaic can be primarily driven by altered plant competitiveness, closely related to the selection of preferred plant species (Crawley, 1983). However, the herbivore's foraging strategy and feeding apparatus is important too. Typically, horses repeatedly crop close to the ground targeting highly palatable shoots and generating "lawns" of graminaceous plants (Fleurance et al., 2011). Cattle, by comparison, snatch at longer and coarser medium-quality forage by wrapping their tongue around the plants (Ungar, 1996, Iason and Van Wieren, 1999) producing a more irregular sward.

4.1.2. Herbage removal and vegetation change

The complex physical changes brought about by grazing and browsing strictly govern the structural and spatial heterogeneity of vegetation (Tainton et al., 1996, Gordon et al., 2004). Herbage removal alters the vegetation complexity through the development of spatial diversity over time (Mouissie et al., 2008). The creation and maintenance of patchiness by grazing can be explained by the positive feedback between selective grazing and plant palatability (Gimingham, 1972, Mouissie et al., 2008). Grazing alters the individual plant or plant parts by modifying its photosynthetic ability, removing biomass and changing its competitive capacity within the community (Olff and Ritchie, 1998) potentially resulting in the plant's growth or death (Lemaire and Chapman, 1996). These direct effects alter the canopy structure and the competitive balance within and between plants, favouring grazing-tolerant plants. By contrast, in ungrazed or abandoned areas the competitive balance shifts to the reactive taller plants, which are often grazing-intolerant, hindering the growth of others (Kohler et al., 2004, Hartley and Mitchell, 2005) reducing structure in the vegetation and resulting in a more uniform sward (Morris, 2000).

Changes to plant species are influenced by grazing-induced patchiness by both horses and cattle (Marion et al., 2010) and selective feeding can modify the competitive relationships between these plants. For example, an increase in diversity is observed in plant communities when species that dominate are selectively fed upon, allowing less competitive species to expand (Crawley, 1983, Bokdam and Gleichman, 2000). Indeed, Charles Darwin remarked that if turf closely browsed by quadrupeds is left ungrazed, the more vigorous plants gradually kill the less vigorous and overall some species perish from competitive response (Darwin, 1906). In some grasslands, associated with lowland heath systems, high-density grazing may increase the number of species by allowing more grazing-tolerant species to spread, as well generating gaps in the sward for new sites for establishment by less competitive species (Bullock et al., 1995, Bullock and Pakeman, 1997).

Lowland heath is vulnerable to the effects of herbage removal because of its halted successional state and specialist plant community (Gimingham, 1972) and negative changes such as loss of dwarf-shrubs have been noted in studies with intensely-grazed systems (Bullock and Pakeman, 1997). Therefore, quantifying the effect of low-density grazing on all habitats within the lowland heath system would contribute to our understanding of this system and help to inform grazing management.

4.1.3. Habitat assemblage influences

The observed effects of herbage removal to the vegetation depend on the type of forage in the habitats, influenced by variables such as nutrient heterogeneity, historical grazing patterns and net primary productivity. This variability between habitats plays an important role in selection by grazers, as has been observed in Chapter 3. For example, the subtle yet significant differences in vegetation communities observed in upland moorland dictated the response of the vegetation to biomass removal (Grant and Armstrong, 1993). Variation in vegetation composition needs careful consideration when selecting a grazing regime for heathland restoration as it can have far-reaching effects to that community (Celaya et al., 2010). Moreover, the spatial and temporal arrangement and availability of nutrients creates heterogeneity in time and space and determines the composition and structure of the vegetation mosaic. Nutrient availability directly relates to the occupancy of the herbivores as they recycle defecated organic matter back into the system (Tainton et al., 1996), although some areas will be avoided. This process governs the community’s rate of new biomass production available for consumption (the net primary productivity or NPP) (Begon et al., 1996). NPP is often higher in plant communities dominated by graminaceous plants like grassland and mire as they have a rapid regenerative ability and a rapid growth response (Hartley and Mitchell, 2005) and it is partly these facets that make grassland and mire attractive to selective grazers (Chapter 3). Grazing by large herbivores has also been shown to be critical for determining plant diversity in habitats with higher productivity (Bakker et al., 2006), an important consideration for habitat restoration.

4.1.4. Low-density grazing

There is much discussion about what level of grazing or herbage removal is most beneficial for conservation management (Grant and Armstrong, 1993, Hearn, 1995), especially on lowland heath (Bullock and Pakeman, 1997, Newton et al., 2009). A number of studies have documented the effectiveness of hard-grazing for maintaining short diverse and herb-rich sward on species-poor habitats (Bullock et al., 1994). Other studies have maintained that a low stocking rate is preferential to preserve a heterogeneous landscape especially for shrub habitat like heathland (Hulme et al., 2003, Pakeman et al., 2003, Fraser et al., 2009), similar to the findings of Chapter 3. There are evidently some scale-issues, but the moderate grazing experienced when using low stocking rates have resulted in a structurally non-uniform and diverse sward in some habitats, although highly dependent on the type and abundance of herbivore in the particular environment (Olff and Ritchie, 1998).

Within a lowland heath system the complex associated plant communities mean it is not possible to maintain an equal stocking level within the different habitat types and for different grazers (De Leeuw and Bakker, 1986). The impacts of herbage removal on the vegetation are highly dependent on the habitat type, the grazing regime, as well as other factors such as size of site, topography, distance to water and forage availability (Bailey, 2004). Nevertheless identifying and utilizing an appropriate stocking rate, and taking into account these factors, is important if grazing is to be employed as a practical management tool. This is especially true when adopted, as they often are, for generating patch-and fine-scale heterogeneity in the sward.

4.1.5. Herbage removal as an effective management tool

Opinions about the effects of grazing or herbage removal for the benefit of conservation of heathland appear conflicting. Positive outcomes include the control of dominating plants, particularly those widespread on heaths, such as purple moor grass (*Molinia caerulea*) (Critchley et al., 2008) and the rehabilitation of dwarf-shrub structure (Hulme et al., 2003). The negative effects have often been attributed to the defoliation and damage of the key plant species (e.g. heather) (Palmer et al., 2003) as well as loss of vegetation structure through uniform grazing (Dennis et al., 2001, Hartley et al., 2003).

The employment of horses and cattle to meet conservation objectives, for those reasons discussed in Chapter 1, is common. However, currently decisions about managing heathland in this way are being made without comprehensive scientific evidence (Bullock and Pakeman, 1997, Newton et al., 2009). A gap in the available knowledge exists, particularly for lowland heath where only few studies review grazing on this system (Bullock and Pakeman, 1997, Lake et al., 2001, Newton et al., 2009). Additionally, there are few studies addressing non-simulated herbage removal for determining vegetation change (Clarke, 1988, Vandvik et al., 2005). Quantifying the actual non-simulated impact on the vegetation in this lowland heath system will enhance our understanding of the changes occurring on these protected reserves. This research will provide scientific evidence for habitat managers to better understand how low-level mixed grazing regimes can restore lowland heath systems.

4.1.6. Quantifying the effects of herbage removal

This study seeks to quantify the impact of herbage removal by low-density mixed grazing (horse and cattle) on lowland heath and to assess the vegetation changes brought about by these large herbivores. The research questions address changes to the architectural parameters of the vegetation (sward height, structure, spatial heterogeneity) and the plant community (plant composition) within four associated heathland habitats (grassland, heath, mire and woodland) brought about by the combined effect of horse and cattle grazing, and are as follows:

(i) Does herbage removal modify the plant community through changes in species composition?

(ii) Is the vegetation sward height within each heathland habitat modified with low-density grazing?

(iii) Are structural and spatial heterogeneity measures enhanced by mixed low-density grazing?

4.2. Methods

4.2.1. Study site and animals

The study was conducted on a lowland heath in north-east Hampshire. Eelmoor Marsh Site of Special Scientific Interest was historically part of a larger system of lowland peat moor (51.274 N; 0.796 W). The site attributes are described fully in Chapter 2 of this thesis, including statutory designations, habitat descriptions and grazing regime, among other site characteristics. Particular site attributes that are of importance for this chapter will be described in more detail here. The habitats classified (grassland, heath, mire and woodland) for this study broadly represent the diversity of habitat assemblages at Eelmoor Marsh and also reflect those of lowland heath more widely.

The site was stocked with small groups of two species: 10 Scottish Highland cattle (*Bos taurus*) and 6 Przewalski's horses (*Equus ferus przewalskii*). The animals were introduced at stocking densities of 0.12 livestock units per hectare (LU/ha) for cattle and 0.08 LU/ha for horses throughout the period of study across the heath system. The livestock were not fed any supplementary forage except during extreme environmental conditions (e.g. heavy snow). Further details are reported in Chapter 2.

4.2.2. Experimental design

Experimental plots were set up to test the effects of low-density grazing (herbage removal and controlling for trampling) in each of the habitat types after the experimental period. Trampling could not be isolated from the design in order to maintain the natural (non-simulated) effect of grazing by the mixed regime. Dunging effects could also not be separated absolutely although dung was removed daily from the plots to minimise the impact of defecation and plots were not placed in or near latrine areas. The experimental plots within the habitats were located within grazing areas and so did not suffer the intensity of trampling to those areas assessed in chapter 5.

The twelve plots consisted of a six by six metre exclosure (control) adjacent to an equal size open naturally-grazed plot (treatment). The plots were set up in May 2008 until September 2011. The vegetation parameters measured in Chapter 5 (Trampling) and Chapter 6 (Dunging) are approximately the same as those measured here (i.e. architectural - sward height, structure and spatial heterogeneity; biological - species composition of the vegetation), although some specific parameters were measured here (grass and gap percentage cover, vertical sward heterogeneity).

Horse and cattle grazing was combined as it was not possible to separate the species-specific grazing effects within the experimental design.

4.2.3. Vegetation sampling

The data sheet for the vegetation parameters recorded is shown in Appendix 5.

Species assemblages

Plant composition was measured using point-intercept frequency measurements (Buttler, 1992). The plant species with the highest number of plant intercepts with the vertical rod was recorded for that point, and provided an accurate measure and count of plant community composition. Species composition data (functional groups and key species), which was used in non-metric multidimensional scaling analyses is displayed in Appendix 6. Functional groups were classified as those detailed in Chapter 2 Methods (*sub-section 2.4.1.1*), and were suited to the dietary plant groups of these ungulates, derived from Chapter 3 and Lamoot et al (2005). Key species were selected based on their abundance within and between habitats, and for their importance in heathland management (*Agrostis* sp., *Festuca* sp., *Juncus* sp., *Molinia* sp., *Carex* sp., *Calluna* sp., *Erica* sp. and *Myrica* sp.) and as food items (identified in Chapter 3 dietary items *section 3.5.*). Methods described in Chapter 2.

Sward height

Sward height was measured (e.g. canopy height) eight times from within each sub-plot. Methods described in Chapter 2.

Structural heterogeneity

Structural heterogeneity and species composition of vascular plants was assessed using point-intercept frequency measurements (Buttler, 1992). Methods described in Chapter 2.

Spatial heterogeneity

The measure of spatial heterogeneity in the horizontal plane was measured in each sub-plot based on the methods detailed in Chapter 2. The estimates of spatial cover of the plant groups provided a rapid means of assessing the herb, grass, legume and other cover which is a more accessible tool for grazing managers to adopt, although a suite of measures would be desirable. Percentage cover indicated the dominance of each plant group as well as the change as a result of herbage removal. Grass cover was of special interest as graminoids were the most favoured dietary plants of both grazers (Chapter 2) and of particular interest for control on protected reserves. Gap cover was adopted as a measure of the creation of gaps and therefore the patch mosaic in the vegetation.

Vertical heterogeneity in the sward was measured by an estimation of percentage vegetation cover within three height strata (less than 20cm, 20-60cm and above 60cm) within each quadrat, following a simplified method of Erdelen (1984) with broader strata. For vertical heterogeneity within each site (i.e. treatment and habitat combination, such as "control grassland") a profile was generated by summing the relative proportion of vegetation cover in each stratum and dividing this sum by the total sum of all proportions (all strata) (Berger and Puettmann, 2000). For each quadrat a profile was also generated by calculating proportional cover within each stratum. Next, the standard calculation of Foliage Height Diversity Index (FHD) was carried out (MacArthur and MacArthur, 1961, Berger and Puettmann, 2000):

$$\mathbf{FHD} = -\sum_{\mathrm{i}} (p_{\mathrm{i}}\, log_{\mathrm{e}}\, p_{\mathrm{i}})$$

where p_i is the proportion of vegetation found in the *i*th strata.

4.2.4. Statistical analyses

The species assemblages were assessed prior to parametric analyses using PRIMER (v.6.1.13) on all sampled plots (Clarke and Warwick, 2001, Clarke and Gorley, 2006). These ordinations examined the approximate dissimilarity of plant species between plots within and between the habitats (grassland, heath, mire, woodland) to compare gradients of habitats (i.e. wet heath and mire) (Gimingham, 1972) and addressed part of research question (i) in this chapter (*sub-section 4.1.6*): does herbage removal modify the plant community through changes in species composition? Plant species diversity (Shannon-Weiner Index) was calculated using the PRIMER software for evaluation with vegetation spatial heterogeneity. Two-way analysis of variance were carried out for the main effects of treatment (grazed and ungrazed) and habitat (grassland, heath, mire and woodland) for the vegetation parameters examining species and functional group composition (research question i). Sward height analyses used the same model addressing research question ii: is the vegetation sward height within each heathland habitat modified with low-density grazing? as well as structure and spatial heterogeneity (research question iii: are structural and spatial heterogeneity measures enhanced by mixed low-density grazing?). For spatial heterogeneity analysis of covariance (ANCOVA) was used to test differences in plant species diversity (Shannon-Weiner Index) between treatments accounting for the effect of Foliage Height diversity (FHD) as a covariate.

Transformations were necessary for positively skewed data: functional groups were transformed using arcsine square-root for the groups, as well as the grass and gap cover, log transformation was used for the key species composition, and for structure a Box-Cox transformation was applied to the counts due to zero-inflated data (Osborne, 2010).

Pteridium was removed from the key species analyses as its presence was minimal in the abundance data and this species was largely avoided by both horses and cattle (M. Wilkie, personal comments).

4.3. Results

4.3.1. Species composition

4.3.1.1. Habitat assemblages

Following the MDS analysis dissimilarity between plots for treatment and habitat was illustrated in the two dimensional ordination and cluster analysis (Figs. 4.1 and 4.2) (raw abundances shown in Appendix 6), addressing research question (i) (*sub-section 4.1.6*). The habitat assemblages separated from one another at around 40 percent similarity except for heath and mire where there was high overlap (Figs. 4.1 and 4.2). This overlap was based on the species composition of both habitats (see section *4.3.1.3. key species* composition). Woodland also separated into two distant groups, with a majority of the differing treatments in each (see section *4.3.1.2 functional group* and *4.3.1.3. key species* analyses). Treatment (grazed) and control (non-grazed) plots showed some separation within the assemblages, quite markedly in grassland and woodland, while only moderately for heath and mire from these visual representation (Fig. 4.1). Outlier groups, such as the grassland satellites around woodland were present and individual species may have determined this (Fig. 4.4). Stress levels indicated that the three-dimensional ordination best represented the assemblage separation (Appendix 7), i.e. approaching 0.10 which indicated an acceptable level of fit for the model (Clarke and Warwick, 2001).

The level of similarity and overlap observed in figure 4.1 demonstrated that the species compositions were similar across all habitats indicating the level of modification to the plant community (research question i) (*sub-section 4.1.6*). Differences between the treatment plots were observed in the cluster analysis dendrogram (Fig. 4.2), illustrating that although the habitat plots were similar, differences existed between grazed and ungrazed plots. For instance, heath (denoted by H) treatment plots (T) separated from control plots (C) at around 60% similarity (in the centre of the dendrogram), which showed overlap was high and similar to the mire plots (Fig. 4.2).

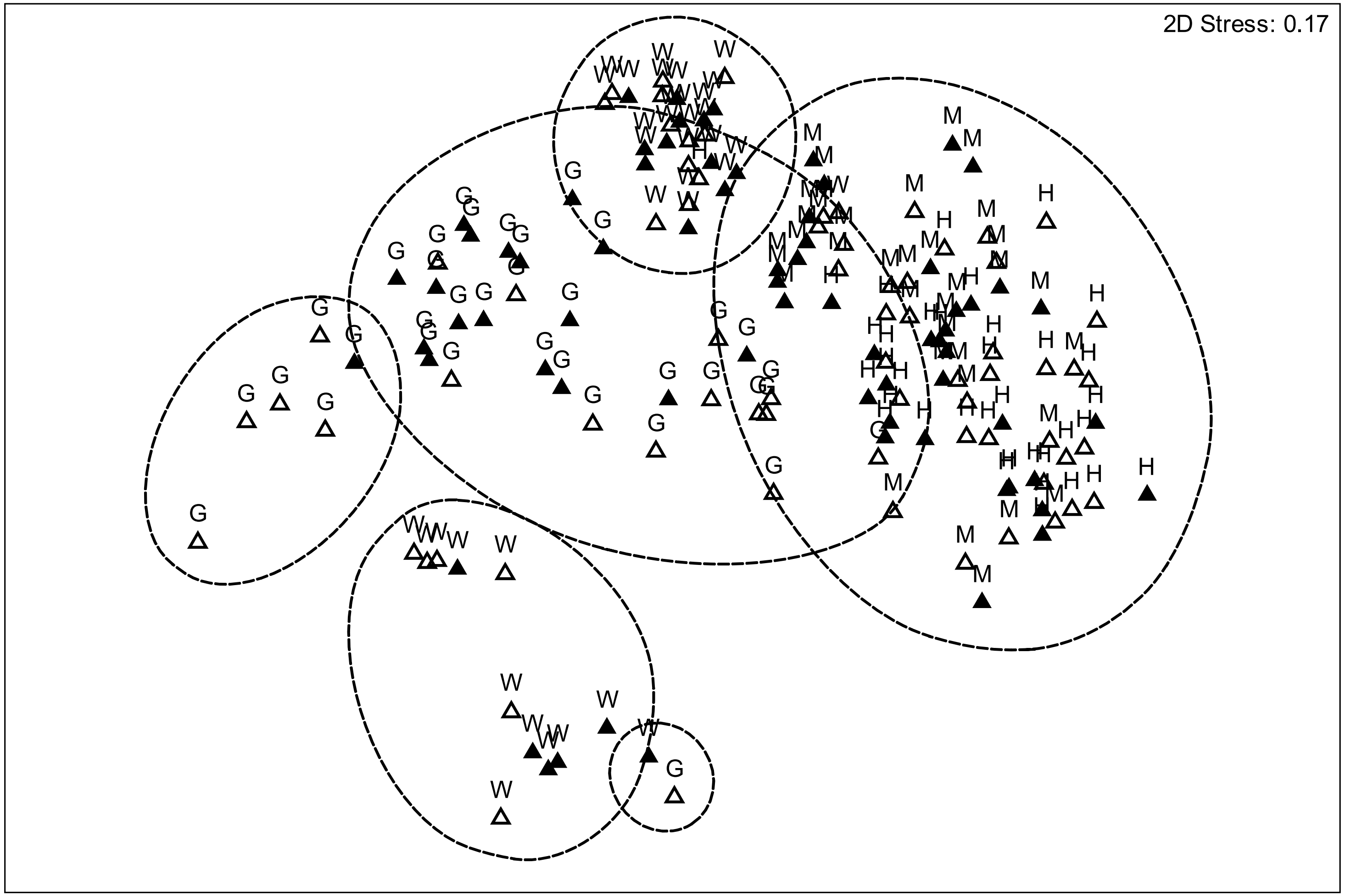


Figure 4.1: Two-dimensional non-metric multidimensional scaling ordination of herbage removal plots for habitat assemblages with treatments and 40% similarity contour (▲treatment plots, Δ control plots; G=Grassland, H=Heath, M=Mire, W=Woodland).

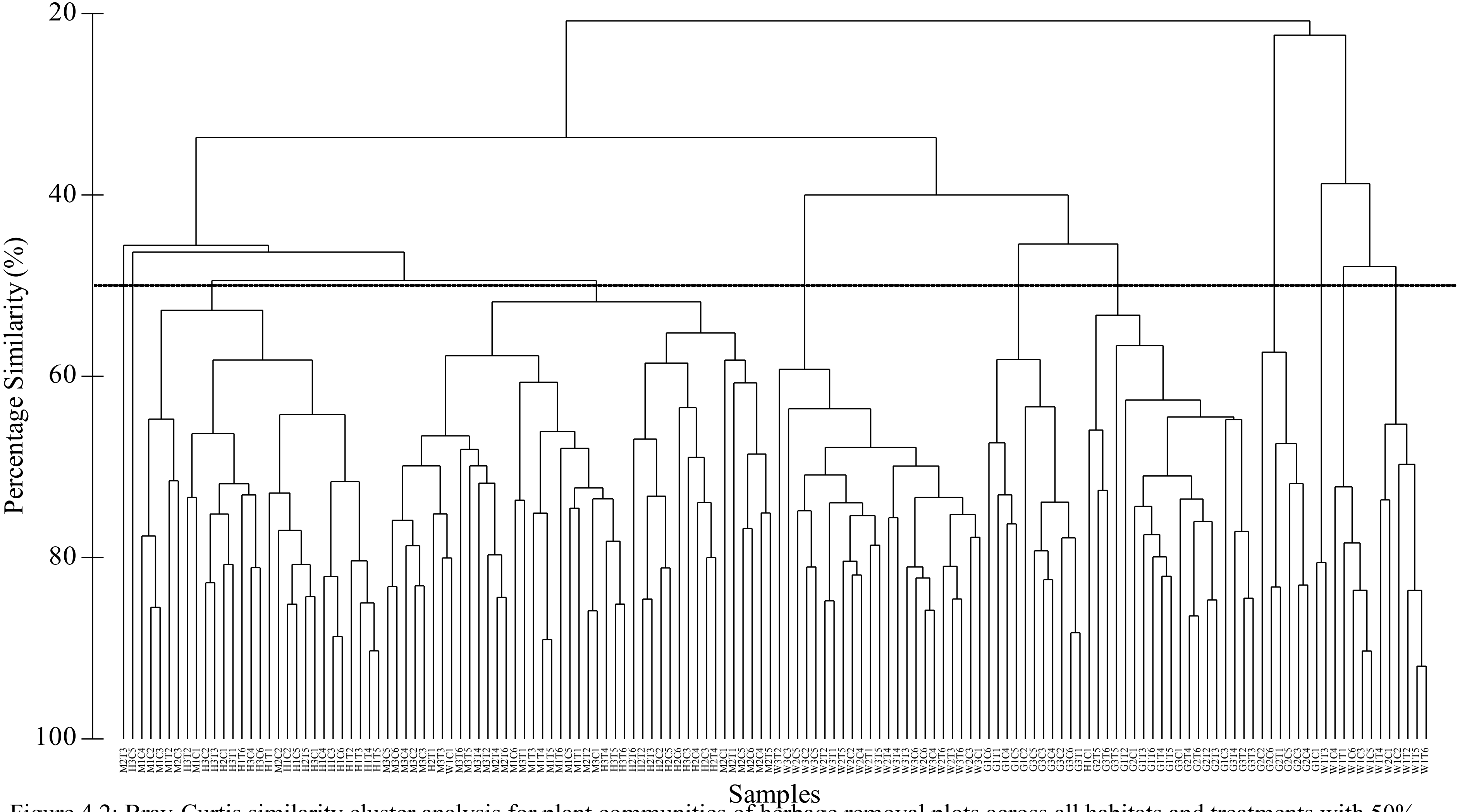


Figure 4.2: Bray-Curtis similarity cluster analysis for plant communities of herbage removal plots across all habitats and treatments with 50% resemblance slice [M: Mire, H: Heath, G: Grassland, W: Woodland; C: Control, T: Treatment; Number: Replicate and sample numbers].

4.3.1.2. Functional groups

Graminoids dominated all habitats but a marginal difference was visible between the control and treatments (ungrazed and grazed), e.g. within grassland (Fig. 4.3). This was supported by a significant difference for this factor treatment (*F*=6.548, *P*=0.012) (Table 4.1) which showed a different response to herbage removal. Minimal differences were observed between the remaining functional group treatments and no significant difference was observed for these. There were significant differences between the sample plots from each habitat, but no interaction (Table 4.1).

Table 4.1: *F*-statistics from two-way ANOVA for proportional functional groups of herbage removal

		Functional groups			
Between-subject effects	*d.f.*	*Graminoids*	*Forbs*	*Woody plants*	*Other plants*
Treatment	1	6.548*	0.287	0.007	0.107
Habitat	3	11.706***	108.998***	133.702***	43.684***
Treatment x Habitat	3	2.592	0.107	1.419	1.931

*Significant at $P<0.05$, **significant at $P<0.01$, ***significant at $P<0.001$

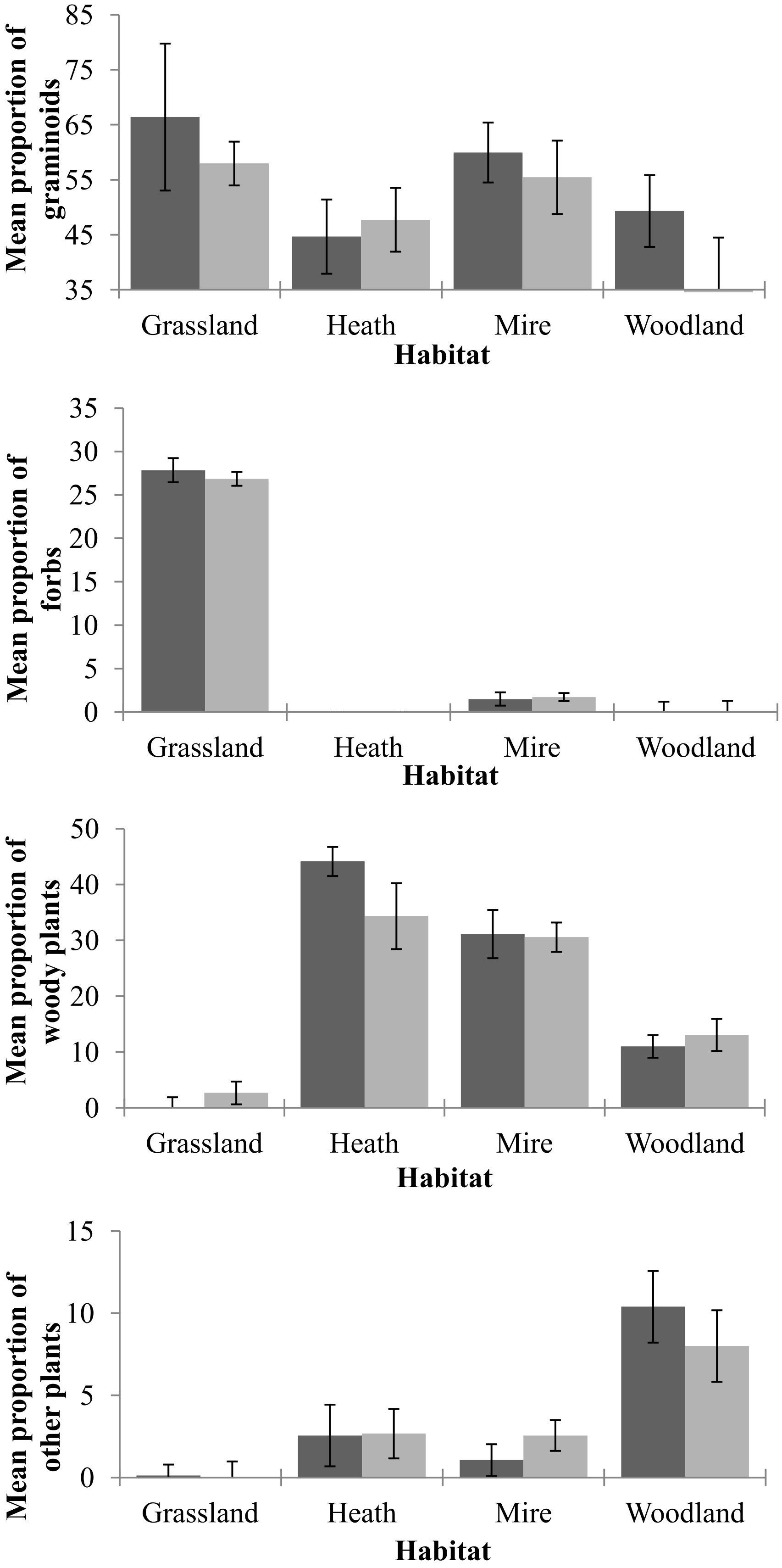
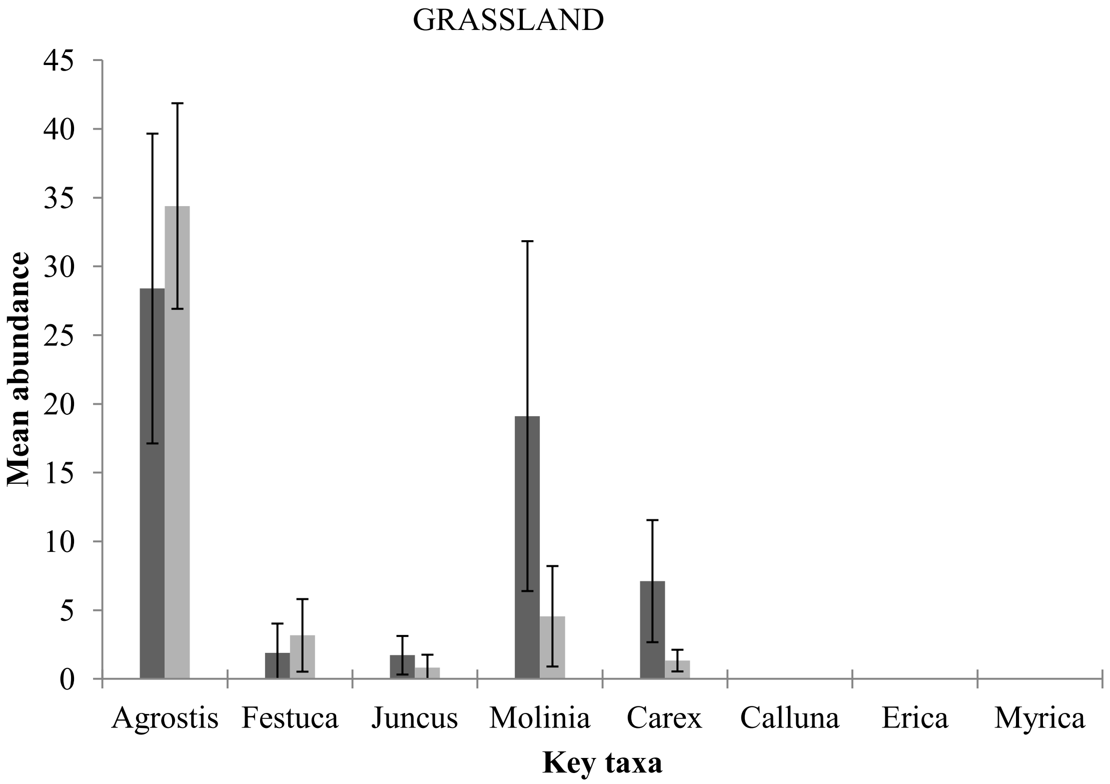


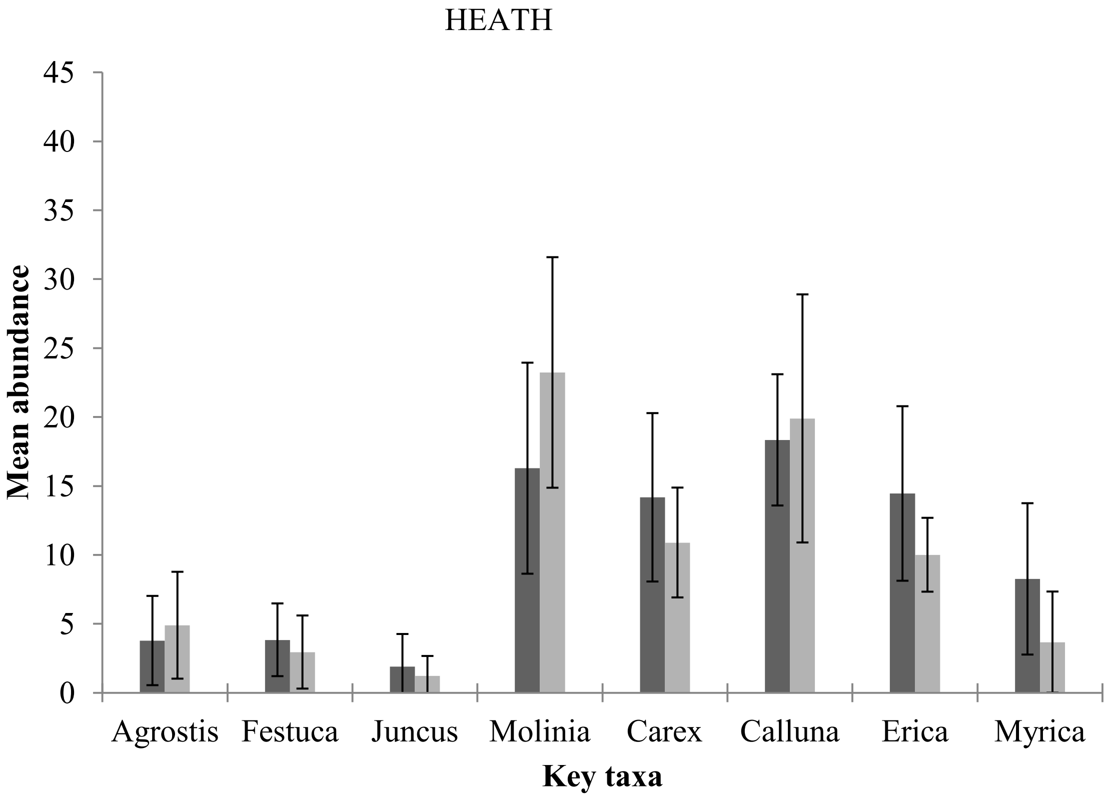
Figure 4.3: Mean proportion functional group compositions (95% CIs) for herbage removal on all habitats. Ungrazed control (dark grey), Grazed treatment (light grey).

4.3.1.3. Key species

The habitats had dissimilar key species compositions. Grass species dominated the grassland habitat, and *Agrostis* sp. which had the highest mean abundance across all habitats and *Molinia* sp. being a major presence (Fig. 4.4). Variance was high for these species within each habitat type. The woody and shrubby species dominated the heath habitat, and the major abundance of *Molinia* sp. indicates why the overlap between grassland, heath and mire existed in the ordinations (Figs. 4.1 and 4.2). Interestingly the woodland displayed a similar composition of the grass species to mire habitat, with *Agrostis* sp., *Festuca* sp. and *Molinia* sp. present; variance of *Agrostis* sp. was larger in woodland than mire (Fig. 4.4).

The analyses revealed significant differences between the control and treatments plots for a number of the key species answering research question (i) (*sub-section 4.1.6*). *Agrostis* responded strongly to herbage removal within mire and woodland, in contrast to the other habitats, although this effect was small with high variances (Fig. 4.4). Table 4.2 illustrated that *Molinia* and *Carex* responded significantly differently for herbage removal with habitat (*Molinia:* F=10.270, P<0.001; *Carex:* F=6.855, P<0.001) (Table 2), supporting the abundances displayed in Figure 4.4. Habitat differences meant these species responded differently within each, such as the opposing effects observed for *Molinia* in grassland and heath (Fig. 4.4).


GRASSLAND
Mean abundance
45
40
35
30
25
20
15
10
5
0
Agrostis
Festuca
Juncus
Molinia
Carex
Calluna
Erica
Myrica
Key taxa


HEATH
Mean abundance
45
40
35
30
25
20
15
10
5
0
Agrostis
Festuca
Juncus
Molinia
Carex
Calluna
Erica
Myrica
Key taxa

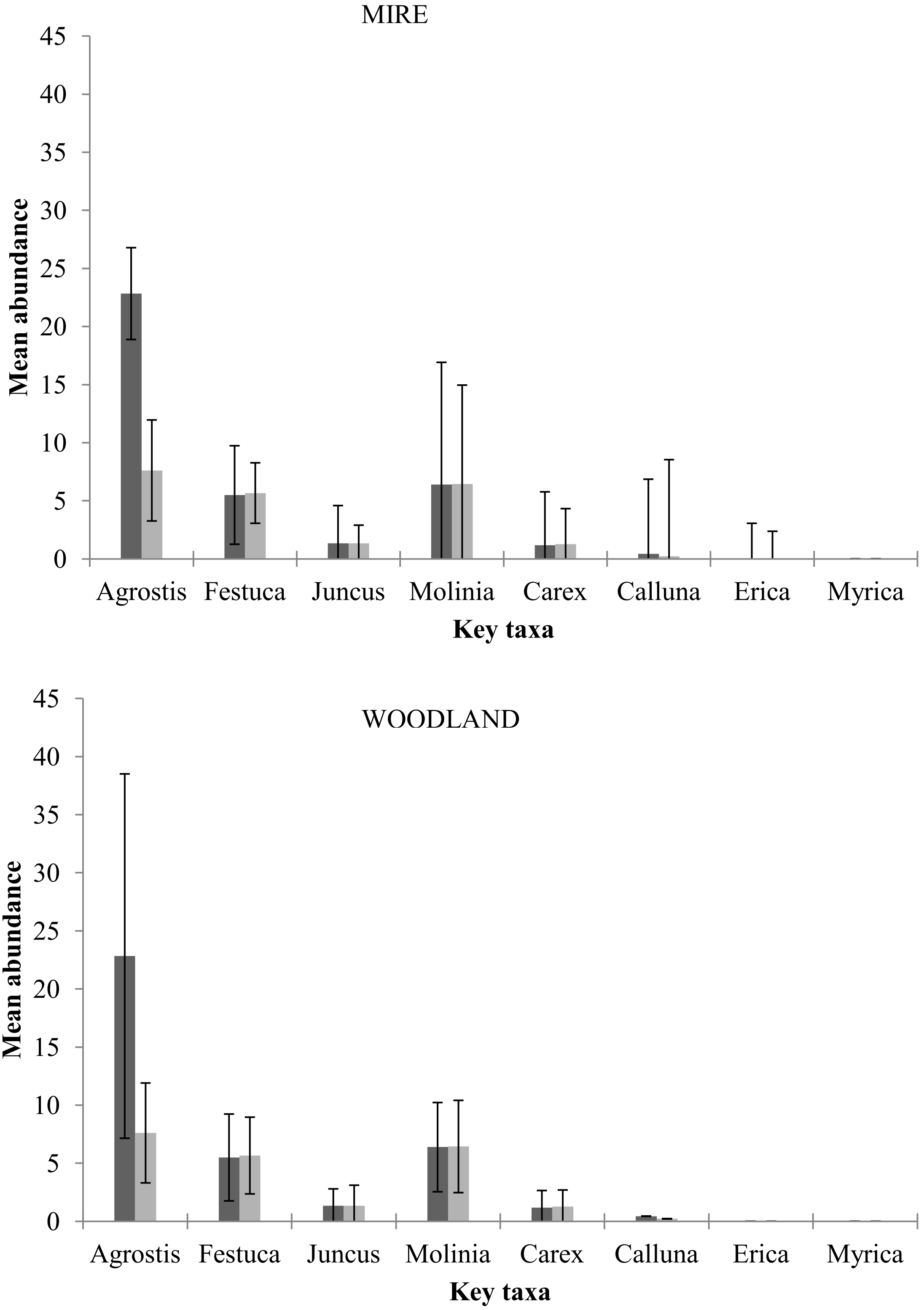


Figure 4.4: Mean abundance of key taxa (with CIs) for herbage removal plots on all associated heathland habitats. Dark grey=control; Light grey=treatment.

Table 4.2: *F*-statistics from two-way ANOVA of key plant species from herbage removal plots across all heathland habitats. *Significant at $P<0.05$, **significant at $P<0.01$, ***significant at $P<0.001$.

Between-subject effects		*d.f.*	*Agrostis*	*Festuca*	*Juncus*	*Molinia*	*Carex*	*Calluna*	*Erica*	*Myrica*
	Treatment	1	26.449***	2.512	0.028	12.272***	18.484***	8.439**	17.472***	5.335*
	Habitat	3	0.218	0.68	0.924	5.664*	29.680***	0.001	11.122**	2.21
	Habitat* Treatment	3	2.452	1.001	0.148	10.270***	6.855***	0.779	2.007	2.063

4.3.2. Sward height

Vegetation height responded differently within each of the heath habitats (Figure 4.5). Dispersion was high for all treatments except for the grazed plots within grassland which showed 50% of observations of canopy height between 2 and 6 centimetres compared to the ungrazed plots for the same habitat between 12 and 28 centimetres (Fig. 4.5). Mire and woodland ungrazed plots showed the highest variance and the abundance of graminoids, especially for *Agrostis* and *Molinia*, would have contributed to this variability in canopy height (Fig. 4.5), as well as some woody plants (Fig. 4.4). Minimal differences were seen between heath grazed and ungrazed plots, with similar inter-quartile ranges and only a few outliers (Fig. 4.5).

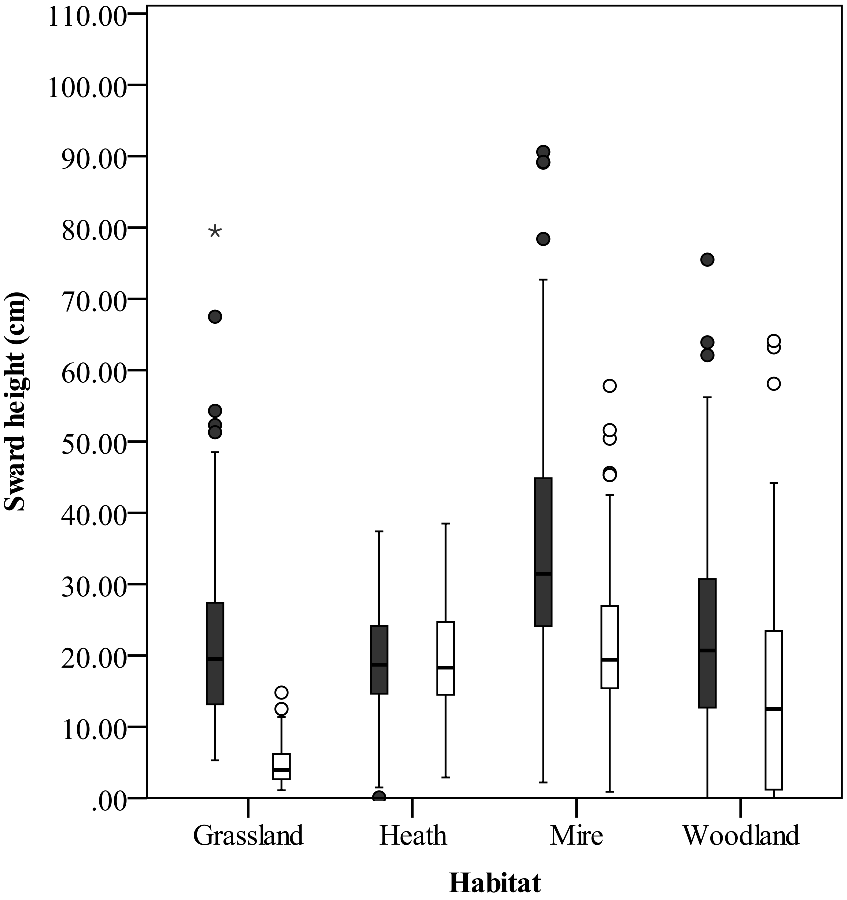


Figure 4.5: Box-plot of sward heights for herbage removal plots for associated heathland habitats (Control=shaded; Treatment=unshaded).

The confidence intervals of the means of sward height were small for all treatments indicating the high confidence that the mean lies within that range (Table 4.3). These also indicated the same trends seen in Figure 4.5, the differential responses of the vegetation to herbage removal.

Table 4.3: Mean sward heights for herbage removal plots for each treatment and controlwithin each habitat with 95% confidence intervals

	Control	CI	Treatment	CI
Grassland	22.03	2.05	4.64	0.42
Heath	19.30	1.23	19.59	1.27
Mire	35.44	2.89	22.18	2.06
Woodland	23.02	2.29	14.04	2.22

A large difference was observed for treatment (*F*=252.585*, P*<0.001) supporting the major decrease in sward height in grazed plots, research question (ii) (*sub-section 4.1.6*), and a marked statistical difference for habitat (*F*=97.214*, P*<0.001) which showed the differing habitat attributes as seen in the species assemblage (Figs. 4.1 and 4.2) and composition (Fig. 4.3) results. The interaction was also highly significant indicating that the vegetation responded differently to herbage removal in each of the habitats (*F*=41.193*, P*<0.001) for this measure of canopy or sward height (Table 4.4). The key species composition analysis also indicated a differential response between habitats, particularly for *Molinia* and *Carex* (Table 4.2).

Table 4.4: *F*-statistics for two-way ANOVA for transformed sward heights (sqaure root) for herbage removal plots (n=1152).

Between-subject effects	*F*-ratio	d.f.	*P*-value
Treatment	252.585	1	0.000
Habitat	97.214	3	0.000
Treatment * Habitat	41.193	3	0.000

4.3.3. Structural heterogeneity

Mire had the highest structural complexity with the highest mean number of structural intercepts, grassland and heath had similar measures of structure while woodland had the lowest structural intercept counts (Fig. 4.6). On mire the ungrazed control plots had a mean number of structural intercepts of 4.93 and the grazed treatment plots had 4.01. The overall lower structural complexity in grassland displayed a differing structural complexity between treatments (control =3.26; treatment = 2.16), followed by heath (control =2.58; treatment = 2.48), and woodland (control =1.96; treatment = 1.35). For grassland, woodland and mire habitats the control plots were more structurally complex than the treatments. In contrast, heath displayed almost equal mean structural intercept values, and supported the sward height findings (Table 4.3 and Fig. 4.5). Confidence intervals were very small and the sample size was very large so caution is noted for analysis.

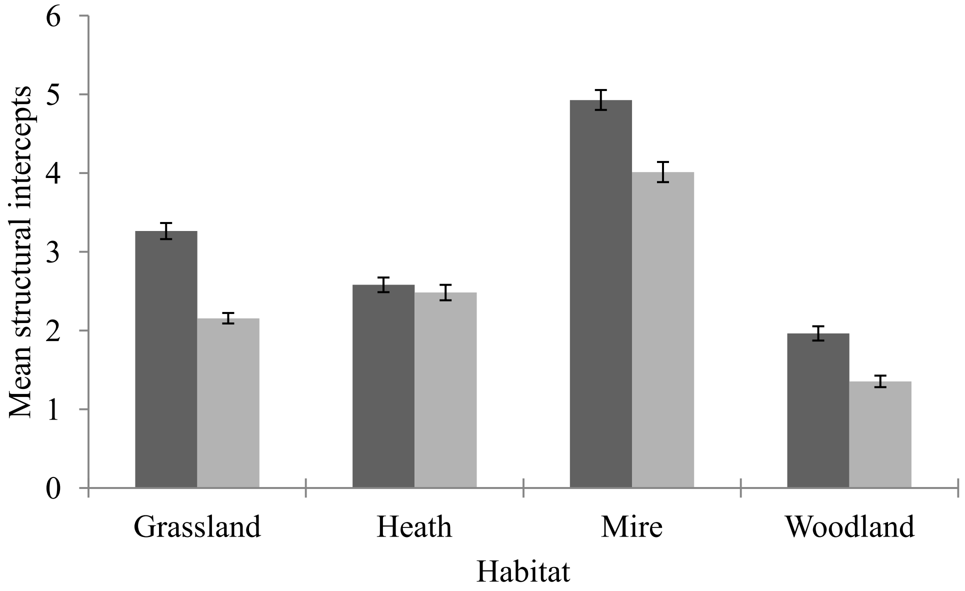


Figure 4.6: Mean number of structural intercepts for herbage removal plots between treatments (Dark grey=control; light grey=treatment) and associated heath habitats (with confidence intervals) (n=9600).

The differences in structural complexity between ungrazed and grazed plots was highly significantly different (*F*=454.372*, P*<0.001) (Table 4.5), answering research question (iii) (*sub-section 4.1.6*), but the vegetation structure was not enhanced. Given the varied responses of the vegetation to herbage removal for each habitat it indicated that there was an interaction between the main factors (*F*=5.969*, P*<0.001). *P*-values were highly significant and *F*-ratios were high for each of the factors and interaction, owing to the large sample size necessary to measure vegetation structure.

Table 4.5: *F*-statistics for two-way ANOVA for structural intercepts for herbage removal plots.

	d.f.	*F*	*P*-value
Between-subject effects			
Treatment	1	454.372	0.000
Habitat	3	908.814	0.000
Treatment x Habitat	3	5.969	0.000

4.3.4. Spatial heterogeneity

4.3.4.1. Grass cover

Grass cover was higher in ungrazed control plots than grazed treatments for grassland, woodland and heath, but these differences were not statistically significant (Fig. 4.7). The findings showed the same pattern for the key species *Molinia* sp. within mire (Fig. 4.4) and illustrated the high abundance of this plant. Control plots were more dominated by grass plants, up to 62.9% in grassland and 35.1% in heath. The confidence intervals indicated that the variability was high for the majority of these treatment plots, especially in mire. Consequently, no significant difference was detected in the treatment effect in two-way analysis of variance (F=2.882, P=0.092) (Table 4.6) nor the interaction effect (F=1.179, P=0.320). Therefore the spatial heterogeneity was not significant enhanced (research question (iii) (*sub-section 4.1.6*) with grass cover as a parameter. The significant difference between habitats was expected (F=8.843, P<0.001), based on the difference in composition reported earlier (*section 4.3.1.*).

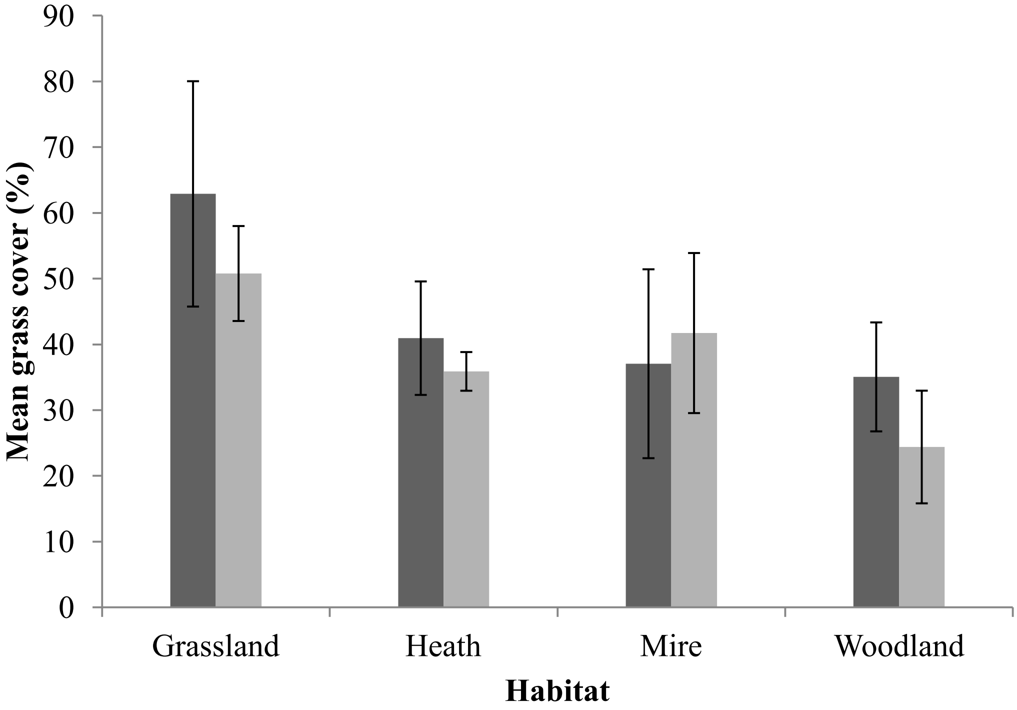


Figure 4.7: Mean percentage grass cover (arcsine) for herbage removal plots in each habitat (with confidence intervals). Control (non-trampled) =dark grey, treatment (trampled) =light grey.

Table 4.6: *F*-statistics two-way ANOVA for percentage grass cover (arcsine transformed) in herbage removal plots

Between-subject effects	*d.f.*	*F*	*P*
Treatment	1	2.882	0.092
Habitat	3	8.843	0.000
Treatment x Habitat	3	1.179	0.320

4.3.4.2. Gap cover

Herbage removal displayed a marked increase in gap cover generated by the presence of grazing stock within all habitats. The magnitude of the effect was greater in grassland than any other habitat (Fig. 4.8). Mire and woodland exhibited the highest mean gap cover and therefore the most open vegetative cover, whilst grassland had the most closed canopy and densely populated sward. As with grass cover habitat selection by the grazers for grassland supported the lowest mean gap cover and highest mean difference.

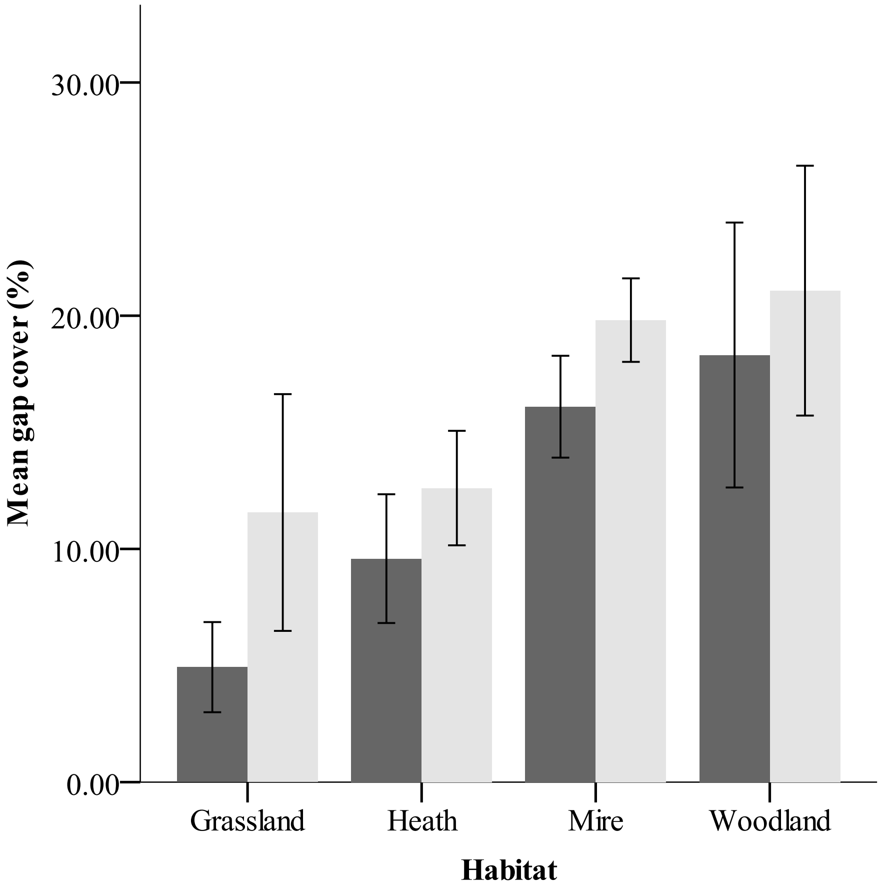


Figure 4.8: Means for percentage gap cover (arcsine) between treatments on each heath habitat (Control=dark grey; treatment=light grey) (n=144). Error bars are 95% confidence intervals.

The results of the two-way analysis of variance supported the difference in means presented above, with a significant difference in grazed treatments (*F*=10.332*, P*=0.002) and habitat effects (*F*=18.928*, P*=0.001). Gap cover did not respond significantly-differently to herbage removal due to habitat (*F*=0.502*, P*=0.681) which was expected given that the responses between all habitats were not different (Table 4.7; Fig 4.8). For gap cover, spatial heterogeneity was enhanced by herbage removal, answering research question (iii) (*sub-section 4.1.6*).

Table 4.7: *F*-statistics for two-way ANOVA for percentage gap cover for herbage removal plots.

Between-subject effects	*d.f.*	*F*	*P*
Treatment	1	10.332	0.002
Habitat	3	18.928	0.000
Treatment x Habitat	3	0.502	0.681

4.3.4.3. Vertical heterogeneity

Calculation of the FHD indices for each site indicated differences in the vertical vegetation profiles between treatments, with a most marked difference in grassland although these were not parametrically tested (Table 4.8). Following calculation of FHD (Appendix 8), Shannon diversity indices based on quadrat were also calculated. The findings of the analysis of covariance indicated that there was no significant departure from the expected, that there was no difference in diversity between grazed and ungrazed plots across habitats, when accounting for the effect of vegetation heterogeneity among strata (Table 4.9). These findings did not support the enhancement of spatial heterogeneity (research question (iii) (*sub-section 4.1.6*). There were no significant interactions between the main effects and the covariate so there was homogeneity of regression slopes. The effect of foliage height diversity (FHD) as a covariate was confirmed to be significant (*F*=5.151, *P*=0.025) and significantly reduced the mean square error of the test for differences in plant species diversity between the main effects. An adjusted *R*-squared value of 0.079 meant that around 8% of the variation of the plant species diversity was explained by the main effects (treatment, habitat).

Table 4.8: Foliage Height Diversity Indices for each treatment plot per habitat for herbage removal plots (Site).

	Control	Treatment
Grassland	0.649	0.016
Heath	0.328	0.395
Mire	0.818	0.577
Woodland	0.684	0.587

Table 4.9: Summary of ANCOVA results for testing the main effects (treatment and habitat) and accounting for vegetation structure (FHD) on plant species diversity (Shannon-Weiner Index) for herbage removal plots.

Between-subject effects	SS	*d.f.*	*MS*	*F*	*P*
FHD	0.806	1	0.806	5.151	0.025
Treatment	0.031	1	0.031	0.199	0.656
Habitat	2.620	3	0.873	5.584	0.001
Treatment x Habitat	0.207	3	0.069	0.440	0.725

Note: R^2*=0.131, Adj* R^2*= 0.079, adjustments based on FHD mean =0.4188. Homogeneity of regressions tested and not significant: F=1.737, P>0.05. FHD regression coefficient=-0.454.*

4.4. Discussion

4.4.1. Modification of vegetation

Low-density mixed grazing had a quantifiable impact on lowland heath and its associated habitats. The results presented in this chapter demonstrated that grazed or ungrazed treatments show distinct characteristics across habitat types. Impacts to architecture (i.e. vegetation height, structure and spatial heterogeneity) were evident (research questions ii and iii), but those that may have influenced plant community composition were not as well defined (research question i).

Vegetation parameters within all the habitats of this lowland heath system were modified by herbage removal to varying degrees. Assessing herbage removal, meant that its precise effects could be quantified and relationships identified, for the first time on lowland heath. Although it was not possible to entirely control the effects of trampling, the experimental plots were located within foraging habitat which was important to capture the grazing variability of the herbivores. The value of measuring actual herbage removal on the study site, which retained trampling, was for the benefit of making real management decisions. The allocation of the experimental plots on grazing areas (derived from Chapter 3), and not intensively trampled areas, meant a different effect was captured in this study. An effect of natural grazing.

Newton et al. (2009) recognised the absence of experimental controls for studies on the herbivore impacts to lowland heath vegetation and this chapter begins to build on quantifying the impacts. The design in this study met the experimental criteria of the study, although a minimal sample size in each habitat was to its detriment. Quantifying herbage removal on lowland heath revealed that there was a well-defined modification of the vegetation through the free-ranging animals. At low grazing densities the impact of herbage removal remained largely heterogeneous, in structure and spatial cover. This measurable change has expanded on the work of some studies which simulated grazing to help understand its individual impacts to vegetation (Britton et al., 2000a, Britton et al., 2000b, Kohler et al., 2004). However, the separation of herbage removal from trampling was difficult here in order to retain natural effects, and should be accounted for in interpretation and when comparing to the aforementioned studies.

Comparisons can be made with some studies (Clarke, 1988, Bokdam and Gleichman, 2000, Vandvik et al., 2005) and follow similar non-simulated methods. In the Netherlands, a heathland grazing study showed minimal effect on grass cover (Bokdam and Gleichman, 2000), like the findings of this study (Table 4.6) and elsewhere similarly species composition was also weakly affected by grazing (Vandvik et al., 2005). The findings broadly answered the first research question that the vegetation was modified. The actual and subtle differences in the sward were explained by architectural (i.e. structural and spatial) parameters in the following sections.

4.4.2. Plant community changes

The plant community within each habitat was altered by the low-density grazing regime, as observed in the assemblage ordinations (Fig 4.1), but parametric analysis revealed that the functional group composition was only clearly defined between the treatments in the graminoids (Table 4.1) (research question i). The high selectivity for graminoids as forage meant this difference was to be expected (Chapter 3), as selection of these grazing-tolerant and competitive plants is widely documented (Fleurance et al., 2001, Palmer et al., 2003, Fraser et al., 2009) creating patchiness in grazed areas (Oom et al., 2008, Marion et al., 2010). The differences were evident within grassland through the creation of short swards (Fig 4.5) by repeated selection by horses maintaining nutritious young growth (Fleurance et al., 2001, Menard et al., 2002), as well as in woodland and its margins where some graminoids were abundant, particularly *Agrostis* sp. (Fig. 4.4). These plants, having an ability to out-compete other functional groups in all habitats, provided explanation for the difference in only this functional group (Crawley, 1983).

Community changes were illustrated in a number of the key species, supporting the findings for the functional groups. The key species, identified as dominant in respective habitat and as food items, demonstrated the changes occurring in the species composition. The mechanisms of competition, mutualism, parasitism and predation (Reid and Hochuli, 2007) could be observed in *Carex* sp. mutually abundant in heath with *Calluna* (Fig 4.4). The ability of *Carex* to grow rapidly and fill gaps meant it displaced other plants while *Calluna,* a woodier, less palatable shrub, was not selected and so was able to persist (Fig 4.4). These processes were similar to those observed in upland moorland between these plants (Hulme et al., 2003) although there was a difference in the study duration. *Molinia* showed similar patterns by responding differently in abundance to grazing across habitats (Table 4.2), supporting the findings of other studies that showed that it becomes difficult for herbivores to break *Molinia* down when at high densities (Mitchell et al., 2008). The findings also demonstrated how this species was able to expand in wet habitats (Critchley et al., 2008) such as in mire and heath (Fig. 4.4). Mire and heath were largely avoided by the grazers (Chapter 3), but on grassland the decline in the abundance of *Molinia* sp., where a more diverse plant community existed, indicated that its competition with other plants is evident and was maintained at a short and palatable height (Fig 4.5) (Hulme et al., 2003).

Grazing-induced changes in vegetation were more distinct in key species than the functional groups owing their selection as preferred food items, and also provide better comparators with other studies which were also studied at this level (Welch and Scott, 1995, Britton et al., 2005, Critchley et al., 2008). Assessment of a wider range of key species would be beneficial for quantifying the effects of low-density grazing on broader plant communities in future studies. The short duration of this experiment also meant only the early stages of vegetation change following herbage removal could be recorded. Therefore increasing the duration of data collection in a repeat of this work might reveal further functional group modifications.

4.4.3. Heterogeneity in the vegetation

The creation of vegetation heterogeneity by herbage removal has often been the objective for many grazing management systems (Gordon et al., 2004) generating available niches and diversifying vegetation through spatial and temporal variation (Jefferies, 1999, Oom et al., 2008). For sward height and structure, heterogeneity was not generated based on the changes by herbage removal but rather from ungrazed control plots, particularly in grassland and mire (Fig. 4.5. and 4.6) which have similar primary productivities (Begon et al., 1996). Herbage removal decreased the canopy height and altered the competitive balance through structural changes (Fig 4.5 and 4.6) which can have knock-on effects for generating variation in the sward (Hartley and Mitchell, 2005). These decreases in canopy height and structure were most marked in grassland where a short cropping of the sward left a structurally-poor vegetation, similar to the creation of “lawns” in the Marais Poitevin, France (Fleurance et al., 2001). The trends in grassland and mire were contrary to the findings of studies which documented an increase in structural complexity by grazing (De Leeuw and Bakker, 1986, Olff and Ritchie, 1998) or in the review by Newton et al. (2009) which remarked on increased structure by low-density grazing (based on information gathered from questionnaire responses) (Newton et al., 2009). The findings did not answer research question (iii) (*sub-section 4.1.6*) if structural complexity is enhanced with grazing, which may be partly explained by the larger spatial scales that the vegetation was examined in other studies (Olff and Ritchie, 1998). Additionally, caution must be noted based on the very large sample size of recorded structural intercepts, as statistical analysis may result in significant differences, but the method was appropriate for the vegetation. Nevertheless, a biological explanation is offered by the rapid increase in canopy density with structure (control plots) that has been observed elsewhere (Hulme et al., 2003) and which correlate with increased height and structural complexity (Table 4.4 and 4.5) (Schwab et al., 2002). The findings indicated that structure is less variable after herbage removal, but this measure is valuable when assessed with the other architectural parameters (e.g. spatial heterogeneity) examining the overall heterogeneity.

In contrast, spatial heterogeneity was generated by a reduction in percentage grass cover and a corresponding increase in gap cover (Figs. 4.7 and 4.8). The findings indicated that the current level of grazing was limiting competitive grasses and enhancing the spatial heterogeneity in the sward, which is a common focus for the recovery of heath communities (Pakeman et al., 2003). The abundance and expansion of *Molinia* sp. in mire (Fig 4.4) explained the increase in grass cover which has been observed in upland heaths (Pakeman et al., 2003, Critchley et al., 2008) and understanding the dynamics of these plants is important for targeted grazing management (e.g. in particular habitats or vegetation communities). Interestingly, the significant increase in gap cover (Fig. 4.8), which is critical for opening sites for colonisation, was unexpected in every habitat but important for continued restoration and for establishing plants (Bullock et al., 1995, Bokdam, 2001). Using these grazing regimes has been documented to favour more diverse communities by creating niches for occupation and enhancing *Calluna* establishment success (Bokdam, 2001, Mitchell et al., 2008), which is often the objective of heathland restoration projects, as it is in the lowland priority habitats.

Grazing-induced heterogeneity can determine plant species diversity, through the generation of available niches and prevention of competitive dominance (Olff and

Ritchie, 1998, Marion et al., 2010) and vertical heterogeneity provided another measure to answer research questions (i and iii). Within different vertical strata changes to the spatial heterogeneity were evident and the Foliage Height Diversity (FHD) Index was increased in controlled plots, which has also been observed in riparian meadow habitat after livestock removal (Dobkin et al., 1998). The mirrored effects in grassland and mire (Table 4.9) were likely related to the plant compositions, but results were not statistically tested so inferences could not be made. When FHD was accounted for in an analysis of plant species diversity (ANCOVA) for herbage removal across habitats, there were no significant differences for the effect of grazing (Table 4.10). This result could have been due to a too broader division of the strata which did not capture the subtle differences in spatial cover although strata were not dissimilar from those assessed in the study of bird communities and vegetation structure (Erdelen, 1984, Dobkin et al., 1998), which showed measureable differences on that scale, so this is unlikely. A weakness in the relationship between plant diversity and grazing-induced heterogeneity may have been a driving factor as observed in wetlands (Marion et al., 2010), so further testing is appropriate.

4.4.4. Variation in habitat and overall impacts

Differences in vegetation following grazing varied between habitat assemblages according to a number of factors such as selection by grazers, the changes to plant community and heterogeneity, as well as other unexamined factors like nutrient availability (Grant and Armstrong, 1993, Ungar, 1996). In grassland and mire the increase in the plant matter in control plots resulted in increased canopy height (Fig. 4.5), enhanced structure (Fig. 4.6) and higher percentage grass cover as compared to treatments (Fig. 4.8) and demonstrated the reactivity of vegetation and the competiveness of plant groups like graminoids (Hulme et al., 2003, Kohler et al., 2004). A less vigorous response was seen in heath and woodland, which were dominated by slower-growing woodier plants (Fig. 4.4), selected to a lesser extent (Chapter 3 *section 3.5.*), unable to rapidly respond and more susceptible to the physical damage of browsing (Celaya et al., 2010). On heath the canopy height and structure remained equal between treatments (Fig 4.5 and 4.6), whilst in woodland there was a decrease in these parameters in grazed areas, but this could be an effect of the combined trampling on *Pteridium* sp., a brittle-stemmed species that constituted a majority of the higher canopy.

Habitat attributes heavily influence the response of the vegetation and the changes induced by the herbivores (Grant and Armstrong, 1993). The chapter has assessed the changes by herbage removal across this lowland heath system describing the detailed modification of vegetation in terms of community and architectural changes, and the heterogeneity generated. The chapter has met the research objective 2 of the thesis for this mechanism (*section 1.11*). It is of considerable value to understand these impacts from this natural mechanism to quantify the effects to aid grazing management for biodiversity in these complex systems.

4.4.5. Implications for grazing management

The results obtained in this study have provided an overall assessment of low-density mixed grazing impacts to lowland heath vegetation. The work has generated data that can be directly inputted into grazing management decisions, specifically for lowland heath, but also for wider applications of nutrient-poor semi-natural habitats because of the diverse vegetation communities within the study site. Quantifying herbage removal alone has meant this highly governing mechanism can be understood in order to address grazing management issues. Moreover the assessment of non-simulated herbage removal was achieved with experimentally-controlled plots, representative of the actual lowland heath dynamics (Newton et al., 2009) which is valuable for its synthesis into practical conservation.

The leading recommendation from this work is based on the impact on graminoids, a major constituent of both herbivores' diet (Chapter 3) and a widespread problem on unimproved lowland habitats. Graminoids can be controlled at low-levels of stocking in target habitats, based on the findings here. This can be extended to all habitats as the sward height data revealed, based on the presence of the mixed grazing regime, although the difference was partially the growth in ungrazed plots and sward height is highly related to structure.

The findings for structural heterogeneity were contrary to those expected and loss in structural complexity, observed across all habitats, meant the vegetation was likely less able to support diverse invertebrate communities (Schwab et al., 2002). Based on just these findings it might be of value to reduce the grazing durations or target grazing to habitats such as mire with very high sward height and structure, but this depends very much on the conservation objectives for the specific site. The related benefit of a loss in structure was the opening of the canopy for other less competitive plants, a highly valuable feature of grazing management. Using similar regimes to this study would reduce the competitive balance of grasses and generate gaps in the sward mosaic. This low-level of grazing also maintained the gaps at an appropriate level without severe disturbance, likely creating space for colonisation by heathland plants. The recommended percentage of gap cover for each habitat requires further evaluation as does its benefits for establishing plant success.

Summary of recommendations based on the study of herbage removal:

- In lowland heath systems with associated grassland and dominating graminaceous plants, a mixed regime of horses and cattle should be used to reduce sward height and control graminoid abundance;
- In wet habitats (e.g. mire) where plants such as *Molinia* sp. are dominating, restrict animal movements within these habitats if possible. On grasslands these plants can be controlled by low-level grazing (~0.2LU/ha), but limit access during sensitive spring growth periods and on both habitats retain some structurally-complex areas (size of areas should be based on site attributes);
- For managers assessing grazing effects on plant abundance, key species should be used to provide a good comparator across habitats;
- A mixed (horse and cattle) low-density regime around 0.2LU/ha should be adopted to limit the spread of grass cover and generate colonising gaps in the sward;
- From the findings of this study and regime, low-density mixed regimes should be employed to retain a level of heterogeneity in the sward based on herbage removal.

The suite of measures used in this study provides an approach to assessing vegetation change by grazing herbivores at the micro-habitat scale, but further work would be best suited to address the larger scale patch-level effects as well, which is of use for the managers on the ground. The management also operates across the broad habitats described (grassland, heath, mire and woodland), so assessment across these should at the very least be adopted, if not at a more detailed vegetation community level (e.g. National Vegetation Classification (NVC) level).

Year-round grazing at a low-density is reported to have negative effects on shoot establishment, being present during the crucial period of March and April (Crawley, 1983), however the control of graminoids, the reduction in canopy height and the creation of gaps meets many conservation objectives and low density grazing mitigates the negative effect. Low-density mixed grazing, based on herbage removal, should be used as a viable tool for controlling dominating plants, but a loss in composition or structural heterogeneity for other higher-order communities which rely on complex vegetation architecture and more diverse foliage strata may occur (Schwab et al., 2002, Dennis et al., 2005, Schaffers et al., 2008).

All three mechanisms (herbage removal, trampling and dunging) should be evaluated collectively before decisions regarding the overall grazing regime are made. These evaluations follow this chapter. Herbage removal, an evidently pivotal mechanism for vegetation change, under a proper grazing regime must maintain or enhance the vegetation of the vulnerable habitat; hence quantifying the real impact is imperative to enable evidence-based decision making of conservation value.

Chapter 5

Physical and compositional changes to lowland heath vegetation by herbivore trampling

Summary

Vegetation and soil changes are dependent on intensity and longevity of trampling while low stocking densities generate a heterogeneous patch mosaic, shaping composition and physical architecture. The mechanism can prevent expansion, create colonisation sites and suppress dominant plants, which are important on conserved systems. At high intensities compaction of the A horizon can be detrimental for vegetation through changes to soil hardness and porosity. The chapter assesses non-simulated trampling impacts of mixed low-density regimes on lowland heath vegetation and asks (i) is plant composition modified at this density?; (ii) are vegetation parameters including structural heterogeneity, canopy height and spatial cover modified with natural trampling?; and (iii) are the physical properties of soil affected in trampled areas by compaction?

Experimental evaluation of trampling on four habitat types at Eelmoor Marsh was undertaken, sampling species composition, sward height, structure and spatial heterogeneity (ANOVA: treatment × habitat). Natural trampling intensity was also quantified in relation to soil compaction (linear regression).

Habitats displayed high similarity within the ordinations (NMDS). The graminoid plant group had significantly lower abundances for trampling and woody plants differed for trampling and habitat, likely due to *Myrica* sp. abundance. Non-trampled plots had significantly higher sward height and structural intercepts. Grass cover was higher in grassland and woodland trampled plots with soil compaction, while gap cover was higher in trampled plots. Soil compaction was significantly different between habitats, but trampling intensity and soil compaction was not significant.

Graminoid dominance (e.g. *Agrostis* sp.), growth, expansion capacity and invasiveness explained the differences in sward height and cover. The associated sward height and structural decrease was due to reduced canopy density. Soil compaction was related to habitat occupancy (Chapter 3) and soil porosity and hardness was likely to have contributed to vegetation change. Long-term evaluation can assess vegetation response and can inform management, illustrating the actual changes brought about by herbivore trampling on lowland heath systems.

5.1. Introduction

5.1.1. Trampling as a key impact mechanism

This chapter examined the effect of low-level trampling on lowland heath plant communities by quantifying the actual vegetation changes to inform grazing management. Among the collective impacts of herbivores, trampling has a visible effect of altering the above-ground physical environment of both the vegetation and the substrate (Bokdam and Gleichman, 2000). The compression of vegetation and compaction of soil is a physical interaction which can alter the productivity of plant and soil rapidly. Intensity and longevity are important factors for the relative impact and a short-lived effect may be temporary (Kohler et al., 2004), but continuous impact has long-term effects on plant composition and soil productivity (Kobayashi et al., 1997). The stocking density of herbivores, particularly on heathland, is an important determinant of the level of this impact. High stocking levels have lead to degradation of upland moorland (Welch and Scott, 1995, Hulme et al., 2003) and sustainable utilisation levels were adopted (Pakeman and Nolan, 2009). Low levels of disturbance are often considered the most suitable practice for grazing and its associated mechanisms, e.g. trampling, because this generates patch-scale vegetation heterogeneity. Changes to these architectural parameters, such as sward height and structure, can also be related to increased plant diversity at low-levels of trampling (Kobayashi et al., 1997, Marion et al., 2010).

5.1.2. Shaping plant communities

The role trampling plays in shaping plant communities can be of equal importance when compared to herbage removal because of the direct effect on habitat composition (Welch and Scott, 1995, Albon et al., 2007), plant morphology or structure, even at low densities (Hester and Baillie, 1998). Plant composition is often altered by trampling, increasing forb abundance on improved grassland (Carvell, 2002) or ericaceous species on upland moorland (Mitchell et al., 2008). On sub-climax heath, plant communities can be rapidly altered by trampling owing to successional species such as *Juncus* sp*.,* readily able to fill the available niches (Critchley et al., 2008). Indeed, trampling pressure prevented *Calluna* expansion and promoted the invasion of *Deschampsia* sp. grass, on fragile heathland in the Netherlands (Bokdam, 2001). In contrast, this disturbance has been shown to be beneficial for suppressing dominant species and allowing promotion of ericaceous species (Mitchell et al., 2008), but it is clear that stocking density is a driving factor (Pakeman and Nolan, 2009).

Trampling impacts on lowland heath have been scarcely studied, although comparisons with upland moorland (Critchley et al., 2008, Mitchell et al., 2008) and heath in continental Europe (Bokdam, 2001) can be made. The documented effects of trampling in other habitat types have been studied such as the simulated effects on mountain pasture (Kohler, 2004) and broadleaf woodland (Mohr et al., 2005), but few studies assess non-simulated trampling effects on lowland heath other than those that quantify a complex of the impacts as ‘grazing’ (Bokdam and Gleichman, 2000).

5.1.3. Physical effect on vegetation structure

Intensively herbivore-managed habitats often maintain a uniform vegetation structure, especially when there is a grass-rich mosaic (Morris, 2000, Striker et al., 2011). It is accepted that localised low-density herbivore disturbance increase the structural heterogeneity of the vegetation (Dennis, 1998, Olff and Ritchie, 1998, Evans et al., 2006, Pavlu et al., 2007), although the magnitude of the effect is commonly related to habitat characteristics. Physical damage to individual plants alters the collective structure of the plants, changing the micro-conditions of that locality (e.g. light absorption of the canopy) and can account for a large degree of the variation in plant species richness (Schwab et al., 2002). These changes may alter successional processes by allowing competitive species to colonise, which can modify the architecture dramatically (Bullock et al., 1995), such as from a woody branching *Calluna*-dominated structure to a densely-tufted sward dominated by *Deschampsia* (Bokdam, 2001). These changes may go hand in hand with changes to the soil substrate and are likely to have knock-on effects to other biological assemblages and habitat complexes.

5.1.4. Heterogeneity and vegetation cover

Relative vegetative cover is strongly associated with the presence of other plant species and also the availability of gaps to colonise or invade (Bullock et al., 1995). Graminaceous species have a high capacity to colonize new areas due to their rapid growth and reproduction when conditions become favourable. Their ability to dominate and compete has dramatic effects on slower-growing plants such as *Calluna* sp., often suppressed by plants such as *Nardus stricta* (mat grass) or *Molinia caerulea* (purple moor-grass) (Roovers et al., 2004, Mitchell et al., 2008). Foraging and trampling-mediated dynamics may create new localities for plants to colonise (Bullock et al., 1995, Critchley et al., 2008). As we are aware from Chapter 4, herbage removal did play a large part in determining spatial cover, i.e. gap availability, but trampling has an altogether different physical impact on vegetation cover because it does not remove the plant or plant part. The impact is therefore very much dependant on the intensity of disturbance (Mitchell et al., 2008). Indeed, the exposure of bare ground can be beneficial for the establishment of seedlings, and valuable for restoration on heath. A low level of disturbance on heathland may introduce a patch-level of heterogeneity in the sward but heavy trampling leads to poaching and degradation of the vegetation (Bardgett et al., 1995) and a shift in vegetation cover can occur reducing trampling-intolerant heather over time (Welch and Scott, 1995, Hester and Baillie, 1998).

5.1.5. Soil structure and properties

The effects of trampling on plants and plant parts are associated with the impacts on soil structure and other physical properties (Hiernaux et al., 1999). Trampling agitates the soil through repeated disturbance or compaction as an animal moves through the environment to meet its ecological requirements (Chapter 3). On heathland the soil structure is composed of podsolic horizons, detailed in Chapter 1, with an upper humus layer (A horizon) of decomposing organic matter where much of the impact from trampling is felt. With limited trampling pressure the soil structure remains intact, providing a suitable medium for germination and nutrient cycling, while increased trampling pressure causes degradation of soil structure and eventually net productivity. These changes can be highly detrimental for germination and can have implications for plant community composition (Gimingham, 1972, Crofts and Jefferson, 1999).

The changes to soil hardness and porosity are often negatively modified through trampling having knock-on effects on plant diversity (Kobayashi et al., 1997). Surface compaction provides a measure of changes to these physical properties. Changes to vegetation and soil are also known to influence the species richness of arthropod populations (Lawton, 1983, Schwab et al., 2002) which are important themselves for maintaining the soil's physical properties (Davidson et al., 2004).

The changing dynamics which have been outlined in other systems and the activity of large herbivores do provide a basis for examining similar trends on lowland heath. It is clear that the changes to the structure, spatial cover and soil properties brought about by trampling are of high importance for lowland heath vegetation assemblages, as it is elsewhere (Hester and Baillie, 1998, Oom et al., 2008).

Many studies of grazing stock quantify trampling impacts to habitats based on simulated manipulations (Kobayashi et al., 1997, Kohler, 2004) and have therefore failed to measure the actual influence of the herbivore to the vegetation. The study here set out to quantify this impact, as other studies on different heath communities have done (Bokdam, 2001, Mitchell et al., 2008). These heathland studies do examine trampling through field experiments, but have not applied experimental exclosures to their design, something of importance for making empirically-based management decisions (Newton et al., 2009). Despite the experimental-design differences between these field assessments and the research here, these studies have been highly informative for management implications of lowland heath vegetation and are relevant to this research.

5.1.6. *Quantifying the effects of trampling*

The aim of this chapter was to quantify the impact of trampling by herbivores on a lowland heath system by assessment of the changes to the vegetation and soil, addressing research question 2 (section *1.11*). The study sought to explore and answer questions about the changes based on the actual effects of trampling, namely:

(i) Is plant composition modified with the presence of low-density herbivore trampling?

(ii) Are vegetation parameters including structural heterogeneity, canopy height and spatial cover modified with natural trampling?

(iii) And are the physical properties of soil affected in trampled areas by compaction through herbivores?

5.2. Methods

Quantifying the impact of natural trampling was central to the management aims of the research. It was not possible to isolate trampling effects from herbage removal and dunging, but these two factors were controlled for in the experimental design by only making assessments in transient areas such as animal tracks or peripheral habitats which were not heavily grazed or used as latrine areas (identified from the data in Chapter 3 and camera-trapping data using Bushnell© camera-trap and Trailmaster©).

5.2.1. Study site and animals

The same habitats were examined at Eelmoor Marsh SSSI as in Chapter 4 (herbage removal). The underlying geology and hydrology (see Chapter 2) of the site were important to the respective impacts on each habitat (habitat attributes described in Chapters 2 and 3). The site was stocked with ten Scottish Highland cattle (*Bos taurus*) and six Przewalski's horses (*Equus ferus przewalskii*). The animals were employed at stocking densities of 0.12 and 0.08 livestock units per hectare (LU/ha) for cattle and horses, respectively. Horse and cattle occupancy, habitat selection (described in Chapter 3) and camera trapping data (Bushnell©, Trailmaster©) made it possible to distinguish areas as predominantly utilised by horse or cattle. These methods also allowed the researcher to outline respective intensity of use. Natural trampling intensity was assessed for each species by examination of the camera trapping data within the respective areas over periods of approximately 6 months (March to September) at each area over three successive years (2009, 2010 and 2011) (Appendix 9).

5.2.2. Experimental design

Three replicates were randomly chosen from the identified trampled areas and experimental field plots set up within each of the habitats (grassland, mire, heath, woodland). Control exclosures were adjacent to the open treatment plots, and were of the same construction as detailed in Chapter 4, fenced in May 2008 to September 2011 for the controlled experimental exclosures. Treatment areas referred to trampled plots and the control areas denoted non-trampled plots.

The vegetation parameters (detailed below) were measured from six sub-plots or quadrats per treatment and control during the growth phases between May and August 2011. All animals were excluded from the control areas from 2008.

5.2.3. Vegetation and soil sampling

The vegetation parameters measured in this chapter are generally the same as Chapter 4, herbage removal (also outlined in Chapter 2), and Chapter 6, dunging. Some specific parameters were measured for each chapter and detailed here. All vegetation records were made in the central 1m^2 sub-plots, leaving a minimum buffer of 0.40cm between sample plots to avoid overlaps and maintain independence. In reality these 1m^2 sub-plots were at least 1metre apart from one another.

Species composition

Within the sub-plots plant composition was measured using point-intercept method (Buttler, 1992). As detailed in Chapter 2, this method recorded plant species as the highest number of plant intercepts of the same species. All plant species were recorded and then grouped as functional groups prior to analysis. Species compositions were used in non-metric multidimensional scaling analyses. Key species were selected from the plant species recorded and identified as those that were dominant or ecologically-important to the respective habitat (*Agrostis* sp., *Festuca* sp., *Juncus* sp., *Molinia* sp., *Carex* sp., *Calluna* sp., *Erica* sp., *Pteridium* sp. and *Myrica* sp.) (See Chapter 2). Methods described in Chapter 2.

Sward height

Sward height was measured (e.g. canopy height) eight times from within each sub-plot by recording directly the top of the canopy. Methods described in Chapter 2.

Structural heterogeneity

Structural heterogeneity and species composition of vascular plants was assessed using point-intercept frequency measurements (Buttler, 1992). Methods described in Chapter 2, and recorded the number of plant parts or plants that intercept the vertical rods of the point frame. This was repeated every 10cm per quarter of the sub-plot to record 100 structural measures per sub-plot.

Spatial heterogeneity

The measure of spatial heterogeneity in the horizontal plane were measured based on the methods detailed in Chapter 2 by an estimation of absolute cover and relative cover of vegetation groups (herb, grass, legume, other cover) for each subplot. Other relative cover was recorded, in particular percentage grass cover and gap cover. The data sheet for the same vegetation parameters is shown in Appendix 5.

Soil sampling

The compaction of the soil substrate was examined using a soil penetrometer (Newton measure (kg per sq metre) measuring the relative resistance of the soil substrate ten times in the each of the six control and six treatment sub-plots per habitat (grassland, mire, heath and woodland). The measures were recorded at the end of the vegetation sampling period in September 2011 on the same day to eliminate systematic and weather-related factors.

5.2.4. Statistical analyses

Natural trampling intensity events were analysed (animal×habitat) using a non-parametric equivalent of the two-way analysis of variance with replication, the Scheirer-Ray-Hare test (SRH), a rank-based test which was suited for the approximately balanced models (Dytham, 2009).

Species assemblage data were analysed with cluster analyses and non-metric multidimensional scaling ordinations using PRIMER (v.6.1.13) (Clarke and Warwick, 2001, Clarke and Gorley, 2006). Analyses included two-way analysis of variance (ANOVA) of the vegetation parameters. Species compositions were analysed as key species and functional groups, which were transformed with arcsine transformed prior to parametric analysis. Sward height data were analysed after a square root transformation. Structural intercepts were transformed to a logarithmic base 10 and anchored at one (Dytham, 2009, Osborne, 2010). An analysis of covariance (ANCOVA) was employed for assessment of percentage grass cover with soil compaction as a covariate. Percentage gap cover data were analysed with two-way ANOVA. Differences in the soil compaction between habitats and treatments were assessed using the same model, following square-root transformation. Linear regression was used to assess the relationship of trampling intensity with the soil compaction properties. A balanced regression model used a random selection of trampling intensity data with the soil compaction data for each habitat.

5.3. Results

5.3.1. Natural trampling intensity

In total, six sites were selected for the initial assessment of natural trampling intensity (Appendix 9). These were representative of the four broad habitat types, based upon the horse and cattle occupancy and habitat selection data from Chapter 3. It was not possible to exclusively select areas only utilised by horses or cattle, but the data from Chapter 3 indicated the most suitable sites. Findings from the camera trapping data of trampling intensity across three successive years (Table 5.1) presented that the number of days when an event occurred varied between animals. This was particularly true on grassland where a large proportion of time was spent foraging on the neighbouring pasture (Chapter 3). The horses had a very high incidence of trampling events for the grassland, whereas in woodland and mire the differences were minimal between species (Table 5.1). The proportions, however, reveal that cattle displayed a higher proportional trampling than horses, and animal factor was significantly different (SRH: SS/MS$_{total}$ =6.74, *P*=0.009, d.f=1), but not for habitat (SS/MS$_{total}$ =7.56, *P*=0.056, d.f=3) or the interaction (SS/MS$_{total}$ =6.08, *P*=0.108, d.f=3).

Table 5.1: Natural trampling intensities for all habitat types (n=total number of events; d= number of days where an event occurred; values (bold) represent the trampling events as a proportion of the number of days where an event occurred).

		Grassland	Heath	Mire	Woodlands
2009	n	647	265	248	318
	d	102	56	68	88
	horse	**6.34**	**4.73**	**3.65**	**3.61**
	n	280	321	337	413
	d	47	70	70	82
	cattle	**5.96**	**4.59**	**4.90**	**5.01**
2010	n	525	452	251	265
	d	109	78	74	76
	horse	**4.82**	**5.80**	**3.39**	**3.49**
	n	491	388	334	305
	d	89	74	73	67
	cattle	**5.52**	**5.24**	**4.58**	**4.55**
2011	n	568	116	213	141
	d	64	31	54	42
	horse	**8.88**	**3.74**	**3.94**	**3.94**
	n	150	79	296	196
	d	25	12	61	46
	cattle	**6.00**	**6.58**	**4.85**	**4.85**

5.3.2. Species composition

5.3.2.1. Habitat assemblages

Cluster analysis displayed similarity between all the habitat assemblages and a high degree of overlap between them (Fig. 5.1). A 50% similarity slice indicated the level at which the samples clustered into those assemblages. Some woodland and grassland sample plots delineated from the assemblages at around 10% and 45% similarity, and may have been due to abundant plant species. The majority of the plots separated into assemblages at 60% although mire, grassland and heath show a high degree of similarity due to originating from the same lineage, at 55% similarity.

The two-dimensional ordination plot resulted in a stress level of 0.19 (Fig. 5.2), and 0.13 for a three-dimensional ordination (shown in Appendix 10) indicating that the ordinations were an adequate representation of the resemblance matrix as they approached 0.10. The dissimilarity between mire and woodland was displayed by the separate clusters almost entirely separate at 60% similarity contour (Fig. 5.2), and as shown in the cluster analysis (Fig. 5.1). There was a high overlap in the clusters observed between grassland and heath, as well as for grassland and mire. The outlying woodland treatment and control plots were likely to be due to a shared key species, specific to that habitat, e.g. *Pteridium* sp. Treatment and control plots were similarly distributed in *n*-dimensional space and there were little distinguishable pattern between grazed and ungrazed plots in this ordination (Fig. 5.2). The similarity between the samples (i.e. similar species compositions and abundances) and high overlap represented did mean the assemblages could be compared directly in the analysis of the vegetation parameters.

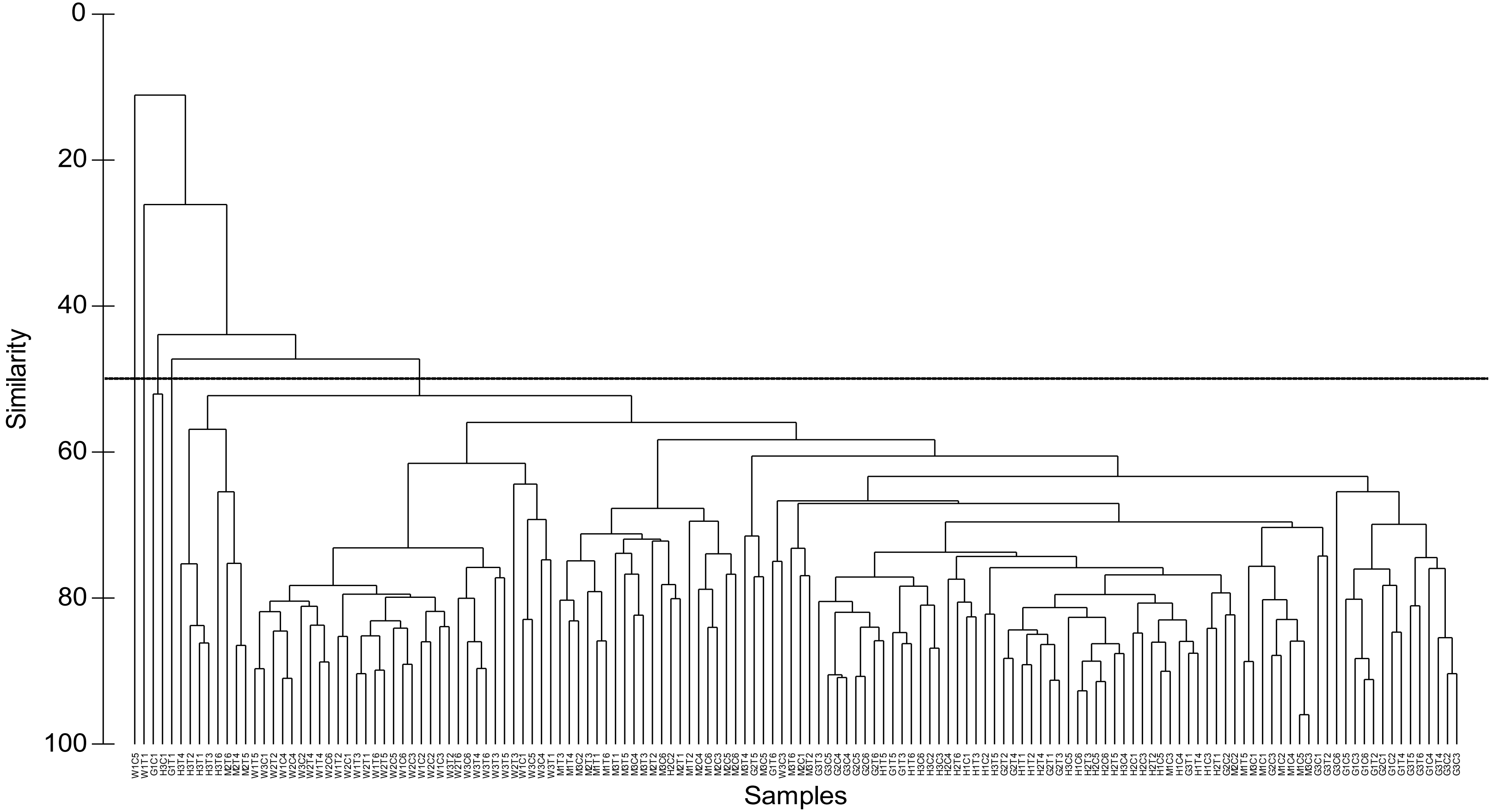


Figure 5.1: Cluster analysis of all trampling plots (samples) within all four habitats (G: Grassland; H: Heath; M: Mire; W: Woodland) for species with indicated 50% similarity slice. Grouping denoted by a CAPITAL LETTER are those plots of the same delineated assemblage grouped together and are above 70% similarity.

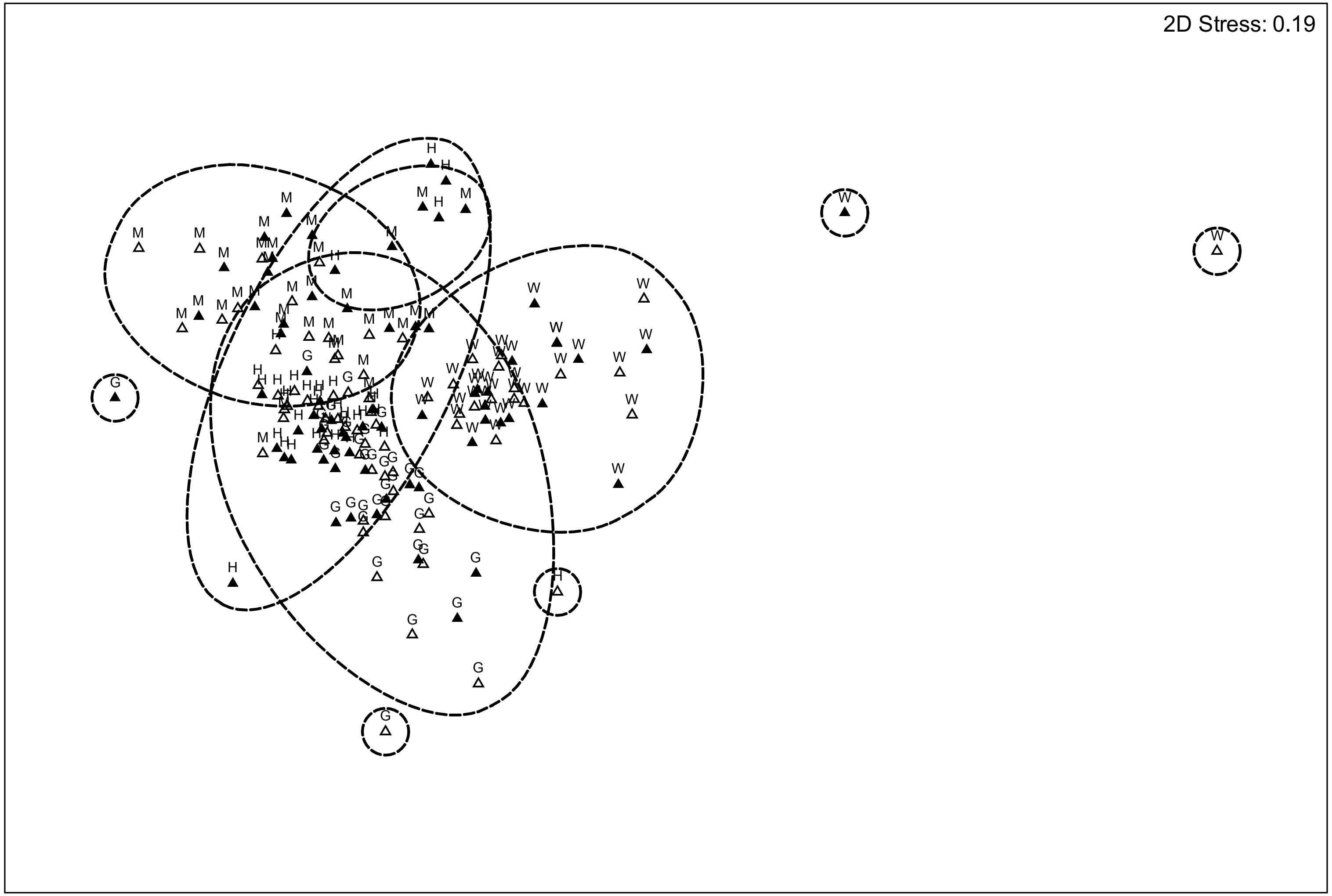


Figure 5.2: Multidimensional scaling ordination for all trampling plots across all habitats (60% resemblance contour shown). (G: Grassland; H: Heath; M: Mire; W: Woodland). ▲ Treatment, Δ Control.

5.3.2.2. Plant functional groups

There was little difference in the proportion of graminoids across the habitats but between treatments there was a significant difference (Table 5.2) (Two-way ANOVA: *F*=5.402, *P*=0.022), a higher proportion observed in non-trampled control plots than trampled treatment plots (Fig. 5.3). There was a clear difference between habitats for forbs, with a large proportion recorded in grassland where there was a higher mean proportion in the non-trampled areas (Table 5.2) (*F*=8.933, *P*<0.001). Woody plants displayed a higher proportion in non-trampled plots in mire, where *Myrica* was abundant (see Fig. 5.4) but the effect was not significant when treatment was assessed alone (*F*=1.251, *P*=0.265). There was a highly significant difference between habitats for woody plants (*F*=48.441, *P*<0.001) and the interaction displayed a significantly different response for habitats (*F*=5.094, *P*=0.002). Little difference was seen between treatments for woody plants on heath despite a high abundance of *Calluna* (Fig. 5.4). Woodland habitat had the highest abundance of other plants (Fig. 5.3) where *Pteridium* was abundant (Fig. 5.4), and a significant difference between habitats was observed (*F*=28.698, *P*<0.001).

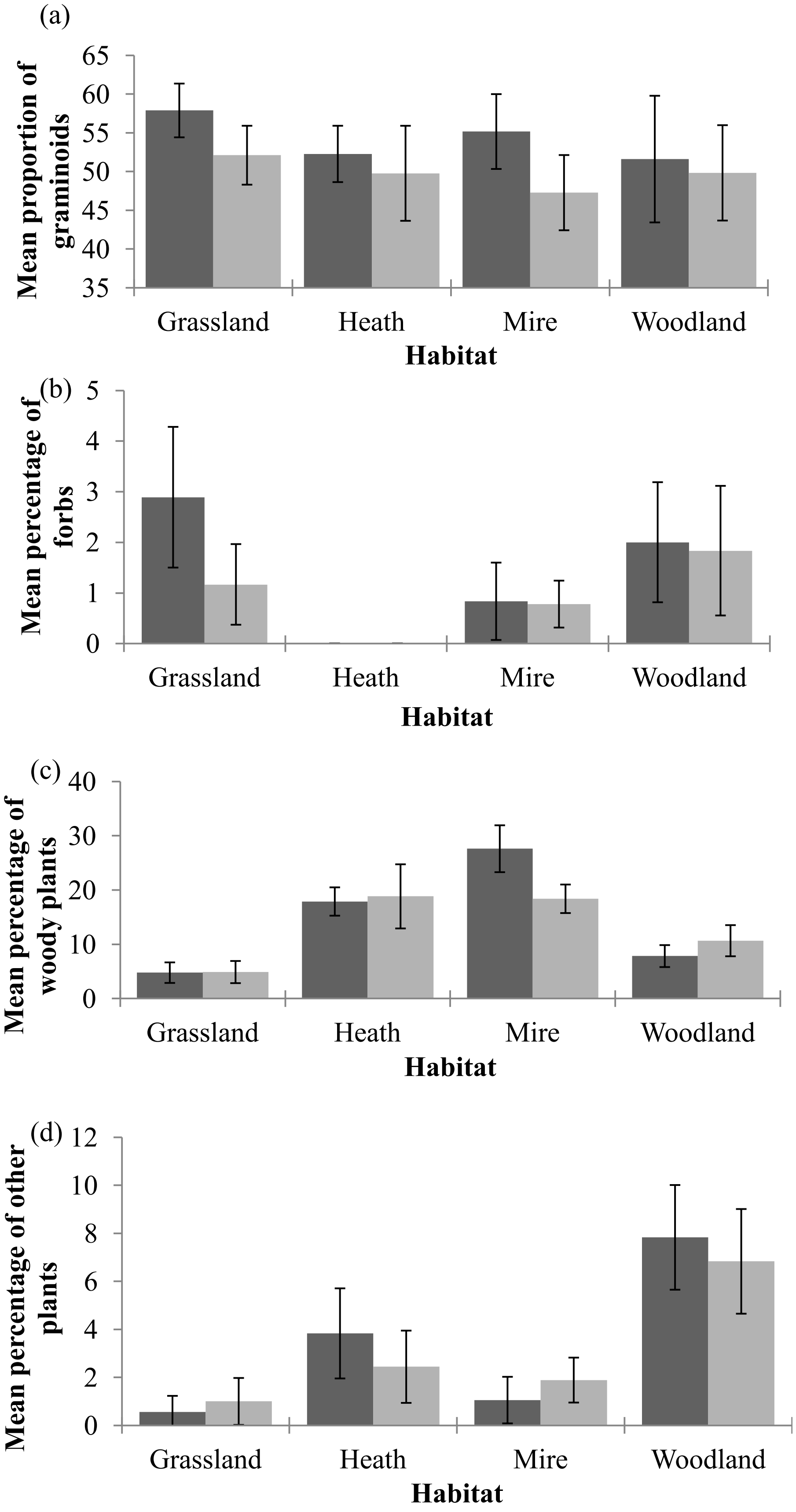


Figure 5.3: Mean proportion of each functional group (arcsine): (a) graminoids, (b) forbs, (c) woody plants, (d) other plants on all habitats (95% confidence intervals) for trampling plots. Dark grey control (non-trampled); light grey treatment (trampled) plots.

Table 5.2: *F*-statistics from two-way ANOVA, between-subjects effects for proportion of functional groups for trampling plots. (*Significant at *P*<0.05, **Significant at *P*<0.01, ***Significant at *P*<0.001)

F-ratios Between-subject effects	*d.f.*	Functional groups *Graminoids*	*Forbs*	*Woody plants*	*Other plants*
Treatment	1	5.402*	2.267	1.251	0.256
Habitat	3	1.090	8.933***	48.441***	28.698***
Treatment x Habitat	3	0.549	1.640	5.094**	0.971

5.3.2.3. Key species

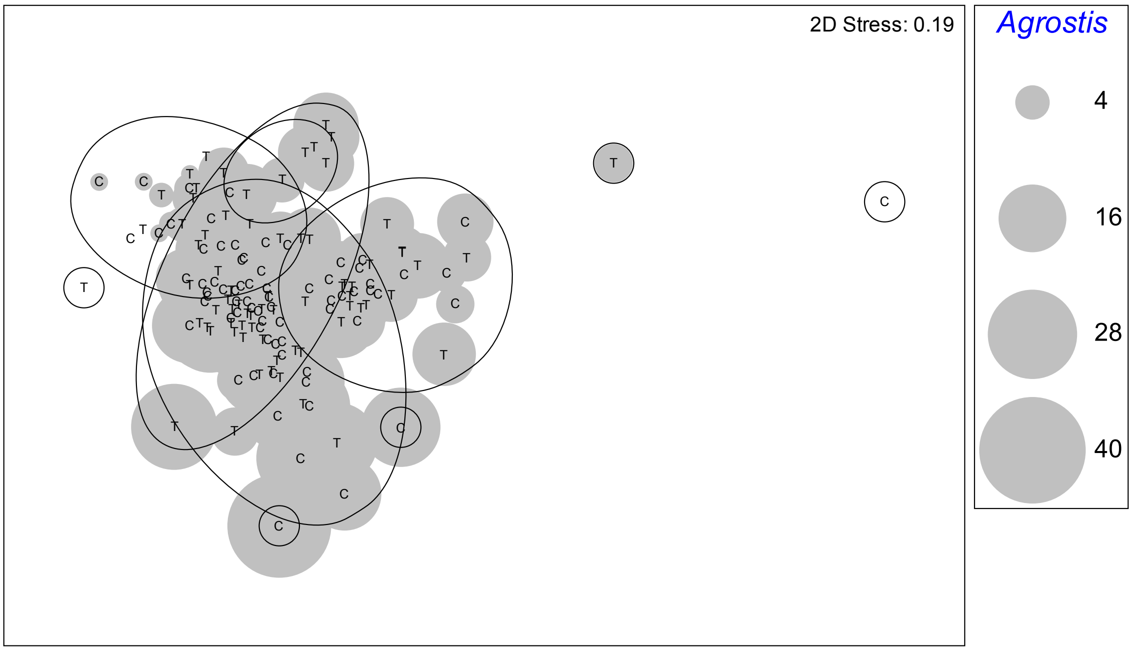
The key species, identified for the purposes of informing management, were dominant in different habitat assemblages displayed by the relative size of the overlaid circles on the habitat two-dimensional ordination (Figs. 5.2 and 5.4). *Agrostis* was widely abundant across the plots in all plots except one grassland plot and one woodland plot. In grassland there was some evidence that this species was more abundant in treatments than controls, but this was not explicit in Figure 5.4. *Myrica,* as expected, was almost exclusively present in the mire habitat, a plant characteristic of this wet habitat, although it did overlap into heath. *Calluna* was abundant throughout all habitats, except woodland when cross-referenced to Figure 5.2, and trends between treatments and controls were difficult to distinguish given the high overlap. There was some evidence of a difference between the abundance of *Pteridium* based on the abundance illustrated in Figure 5.4, and this species was almost entirely present in woodland.

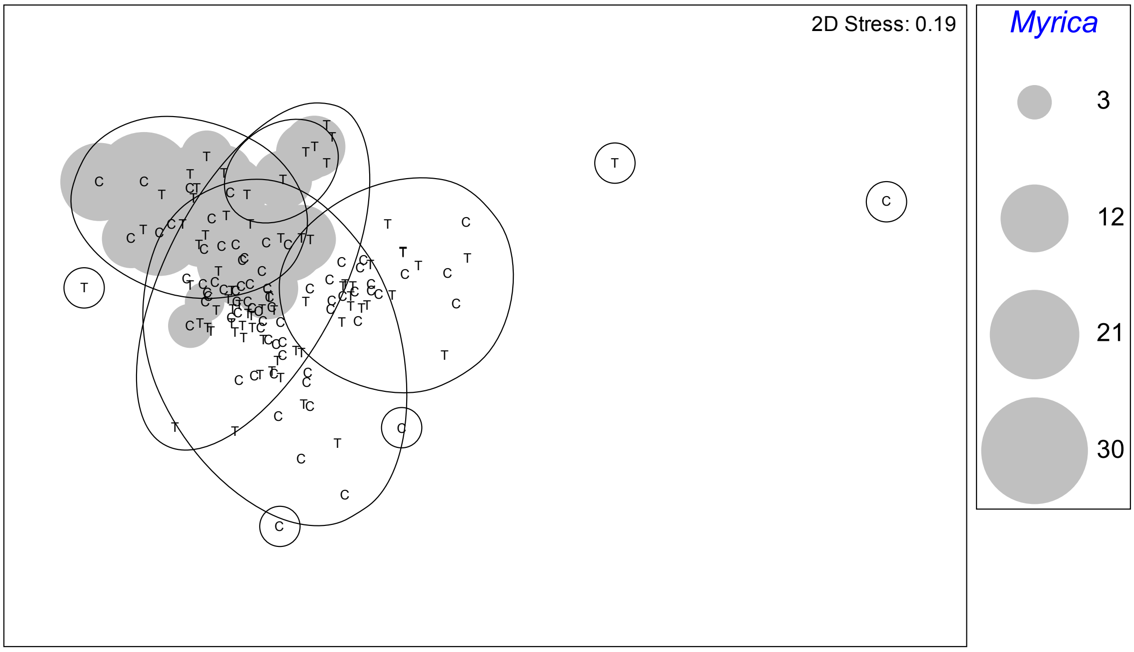
It was clear from the highly significant differences in the key species (e.g. *Calluna* sp., *Erica* sp., *Myrica* sp. *and Pteridium* sp.) for habitat that the species were dominant within respective habitats (Table 5.3). No significant differences were observed for the main effect of treatment or the interaction terms.

Table 5.3: *F*-statistics for between-subject effects for key species for trampling.

(*Significant at $P<0.05$, **Significant at $P<0.01$, ***Significant at $P<0.001$)

			Key taxa								
Between-subject effects		*d.f.*	*Agrostis*	*Festuca*	*Juncus*	*Molinia*	*Carex*	*Calluna*	*Erica*	*Pteridium*	*Myrica*
	Treatment	1	0.018	0.011	0.032	0.231	0.68	0.082	0	0.235	0.026
	Habitat	3	0.42	0.091	1.713	0.241	1.834	61.844***	19.001***	12.141***	513.443***
	Treatment x Habitat	3	0.061	0.024	0.013	0.041	0.591	0.067	0.099	0.207	0.026


2D Stress: 0.19
Agrostis
4
16
28
40
C
T


2D Stress: 0.19
Myrica
3
12
21
30
C
T

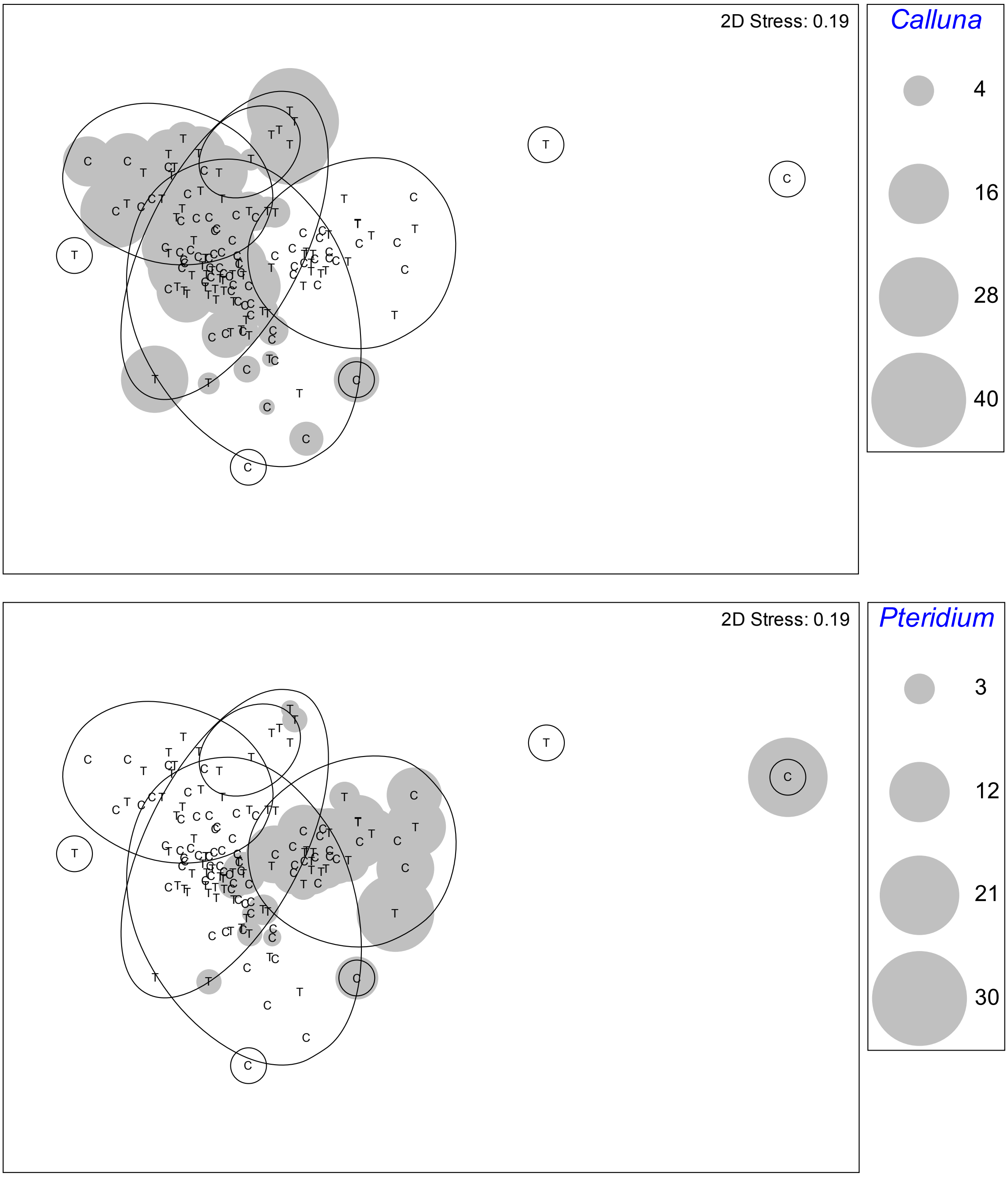


Figure 5.4: Two-dimensional ordination plots of key species abundance from within all trampling plots for *Agrostis, Myrica*, *Calluna* and *Pteridium,* with plots dominated by key species highlighted. T: treatment (trampled plots); C: control (non-trampled plots).

5.3.3. Sward height

Trampling had a marked effect on the sward height of the vegetation as shown by the mean differences between treatments in all habitats except woodland (Fig. 5.5). Grassland and heath showed differences in mean sward height of 51% and 34%, respectively, between treatments. The variances displayed that the means were highly different in all habitats except woodland. Mire habitat showed a major response in height for non-trampled control plots, 154% higher than trampled treatment plots.

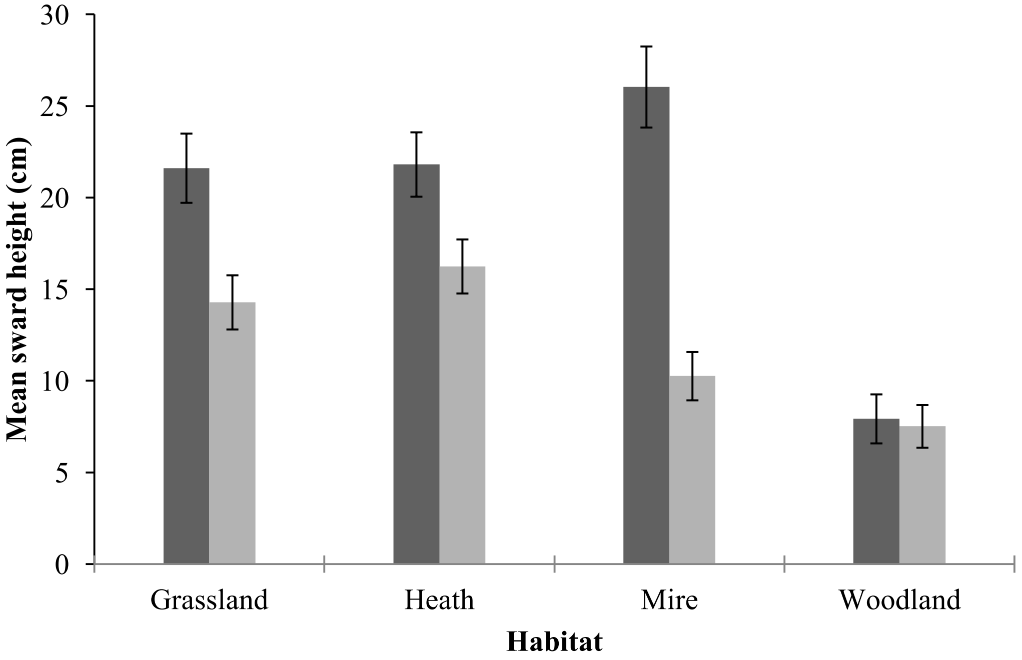


Figure 5.5: Mean sward heights for control (non-trampled plots) and treatment (trampled plots) per habitat with confidence intervals. Dark shade (control), light shade (treatment)

Analysis indicated that there was a significant difference between groups for both of the main effects. Trampling plots demonstrated significantly lower sward heights than the non-trampled control plots (F=6.654, P=0.010) and a highly significant difference was apparent between habitats (F=95.081, P<0.001) (Table 5.4). The interaction effect indicated that the sward height responded significantly differently to trampling between the four habitats (F=17.068, P<0.001) (Table 5.4). Figure 5.5 revealed that between grassland, heath and mire there were differential effects for trampling. Woodland evidently had a minimal response to trampling (Fig. 5.5) and the plant functional group composition (Fig. 5.3) indicated a differential plant composition.

Table 5.4: *F*-statistics from two-way ANOVA for between-subject effects for sward height for trampling plots (n=1152)

Between-subject effects	F-ratio	d.f.	*P*-value
Treatment	6.654	1	0.010
Habitat	95.081	3	0.000
Treatment × Habitat	17.068	3	0.000

5.3.4. Structural heterogeneity

Between treatments in grassland and mire there were significant differences in structural heterogeneity (Fig. 5.6 and Table 5.5). The differences in structural heterogeneity correspond to the sward height for the respective habitats, and there was minimal change in height or structure for woodland plots. Non-trampled control plots were twice as structurally-complex as the treatment plots for mire, but in contrast, only a difference of a tenth was displayed in the woodland. The very small confidence intervals indicated a high certainty of where the mean lies in all factor levels, although the sample size was high (n=9600). Treatment and habitat were both significantly different for the two-way ANOVA (treatment: F=333.933*,* P<0.001; habitat: F=7.674, P<0.001*)*. The interaction (treatment x habitat: F=71.530, P<0.001) also showed that non-trampled and trampled plots responded differently according to habitat (Table 5.5). This was most marked between the mire and other habitats for treatments and controls, and with strong opposite effects between mire and the other habitat types (Fig. 5.6). This was backed by the sward height data (Fig. 5.5), but other interaction effects were presented between the other habitats.

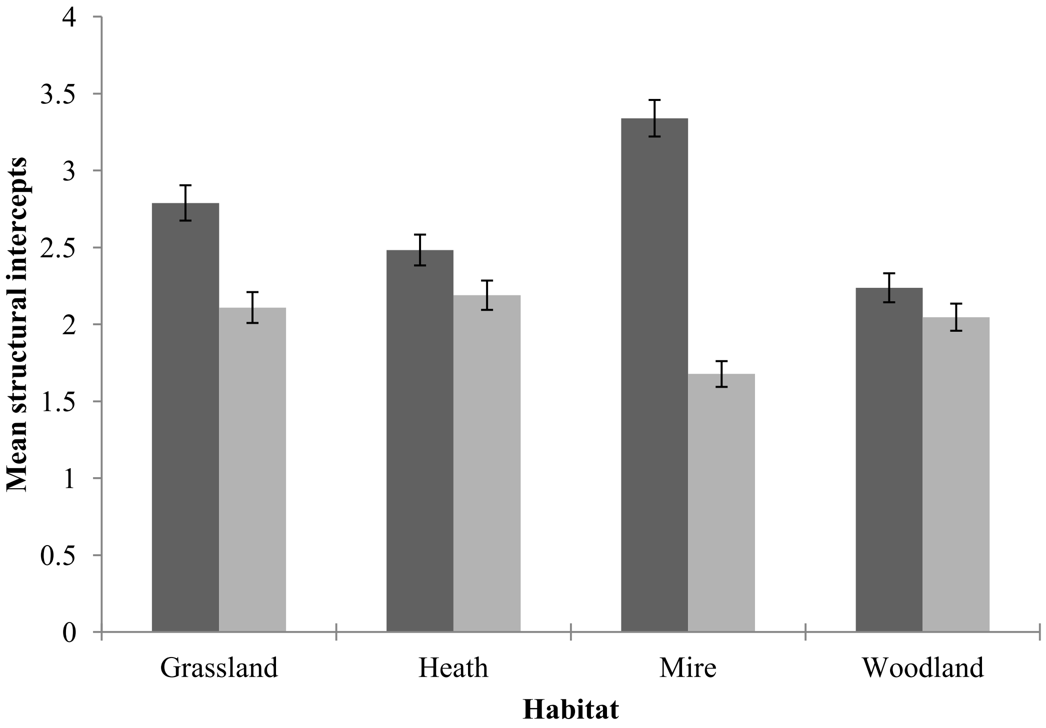


Figure 5.6: Mean structural intercepts for trampling plots per habitat with confidence intervals. Dark shade (control – non-trampled), light shade (treatment - trampled) (n=9600).

Table 5.5: *F*-statistics from two-way ANOVA for between-subject effects for structural heterogeneity for trampling plots

Between-subject effects	*d.f.*	*F*	*P*-value
Treatment	1	333.933	0.000
Habitat	3	7.674	0.000
Treatment x Habitat	3	71.530	0.000

5.3.5. Spatial heterogeneity

5.3.5.1. Functional plant group cover

The subtle changes in the spatial cover of functional groups between treatments are shown in Figure 5.7. Each habitat type displayed typical cover for that assemblage, such as a very high proportion of other plants in heath (including woody plants such as

Calluna). These charts should be examined with Figure 5.3, which best demonstrated the vegetation composition of these functional groups.

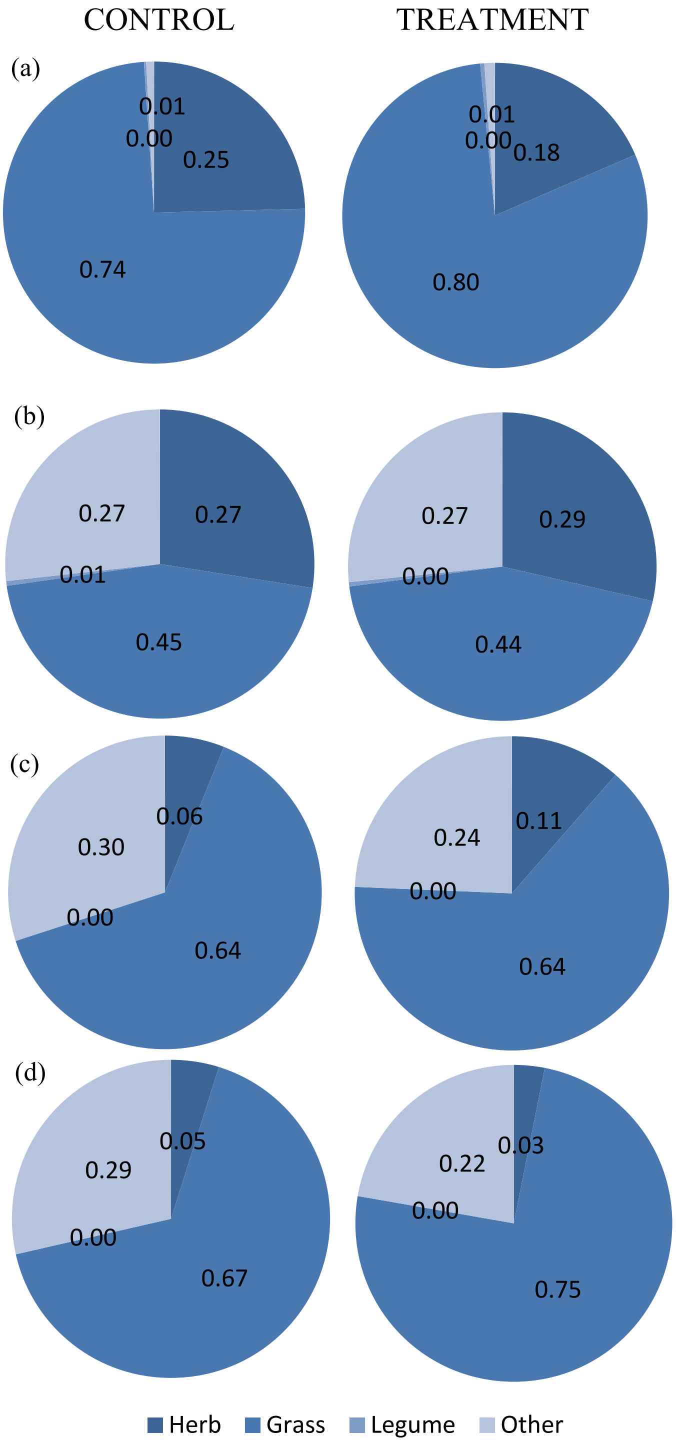


Figure 5.7: Mean percentage functional group cover for trampling plots: (a) Grassland ; (b) Heath ; (c) Mire ; (d) Woodland. Control (non-trampled) (left), Treatment (trampled) (right). Data labels show proportional cover.

Percentage grass cover, which provided a good estimate of the dominance and invasiveness of grasses, showed that woodland had the most marked change in grass dominance due to the effect of trampling (Table 5.6). In grassland the increase in grass cover was at the expense of herb cover (Fig. 5.7). From visual inspection of the means, the other habitats showed little change in the dominance of grasses based on the natural trampling level, e.g. mire and heath showed negligible change, although the variances were moderate.

5.3.5.2. Grass cover

Analysis of covariance revealed a significant difference between habitats for grass cover (*F* = 69.154, *P*<0.001) with soil compaction as a covariate (detailed later, *see section 5.3.6*) which was not significant (*P*>0.05) (Table 5.7) and therefore did not reduce the mean square error of the test for differences in grass cover between the main effects. A significant difference between the treatment effect (*F* = 4.190, *P*=0.045) presented a differing response of grass cover between the non-trampled and trampled plots. The observed response of grass cover in some habitats did not correspond with the decrease in graminoids on trampled plots seen previously (Fig. 5.3).

Table 5.6: Mean percentage grass cover with confidence intervals (CI) for all trampling plots. Control (non-trampled), treatment (trampled)

	Control	CI	Treatment	CI
Grassland	74.33	±4.62	79.94	±4.38
Mire	64.94	±6.05	64.22	±5.58
Heath	45.00	±2.99	44.72	±3.82
Woodland	66.89	±3.01	74.22	±3.51

Table 5.7: Two-way ANCOVA for grass cover (arcsine) with soil compaction (square-root) covariate for all trampling plots

Between-subject effects	*d.f.*	*F*	*P*
Soil compaction	1	0.289	0.592
Treatment	1	4.109	0.045
Habitat	3	69.154	0.000
Treatment x Habitat	3	1.750	0.160

R^2=0.623, Adj R^2= 0.601.

5.3.5.3. Gap cover

Percentage gap cover, indicating proportion of gaps created by trampling, presented marked differences between trampled and non-trampled plots. In all habitats there was a higher proportion of gap cover in trampled plots than in non-trampled plots, although woodland displayed a minimal difference with moderate confidence intervals (Fig. 5.8). Treatment had a significant effect on gap cover (*F* = 26.912, *P*<0.001). For habitat and treatment no significant interaction was shown (*F* = 2.409, *P*=0.070) (Table 5.8) despite woodland habitat responding differently to the other habitats for treatment in Figure 5.8.

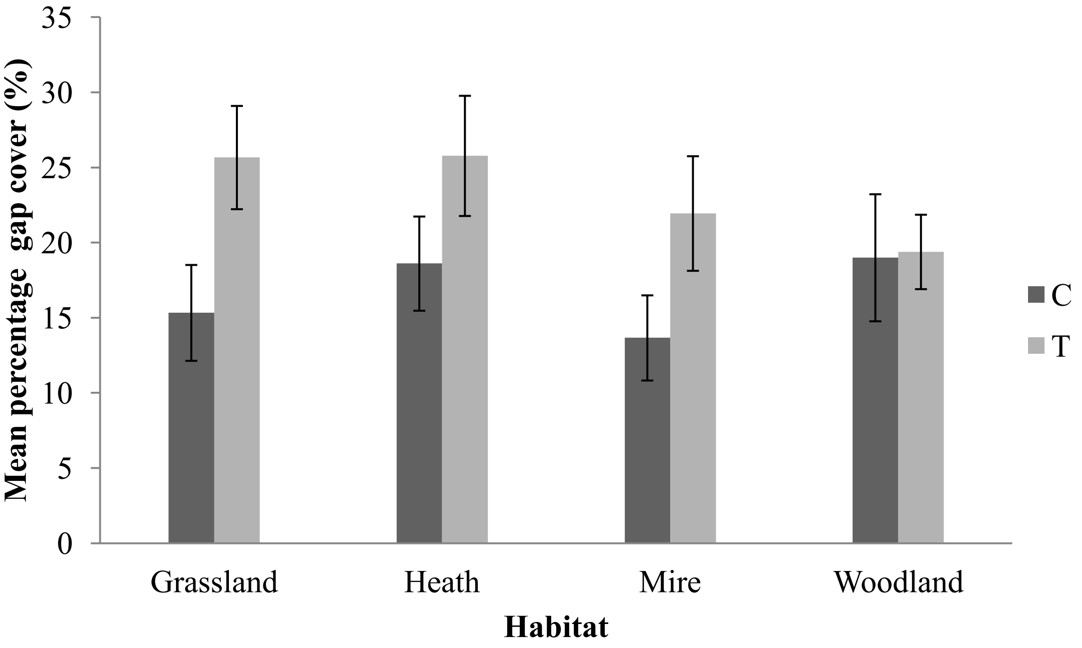


Figure 5.8: Mean percentage gap cover for all trampling plots for each habitat with confidence intervals. Control (non-trampled); Treatment (trampled).

Table 5.8: *F*-statistics from two-way ANOVA for between -subject effects for percentage gap cover (arcsine) for all trampling plots

Between-subject effects	*d.f.*	*F*	*P*
Treatment	1	26.912	0.000
Habitat	3	2.081	0.106
Treatment x Habitat	3	2.409	0.070

5.3.6. Physical soil assessment

Comparison of the mean soil compaction values measured across all habitats displayed a significant difference between the habitats (Table 5.9) (habitat: *F*=22.269*, P*<0.001) and for the interaction (treatment×habitat: *F=37.762, P*<0.001), but not for treatment (*F=1.125, P*=0.289) (Table 5.10). The findings support the behavioural data from Chapter 3 which indicated that grasslands were the most commonly occupied habitats for foraging and the adjacent areas had the highest observed level of soil compaction and intensity of trampling (Table 5.1). Trampled areas were also all higher than controls, although the confidence intervals indicate there was some overlap in variance (Table 5.9), and hence non-significant difference for treatment.

Table 5.9: Mean compaction of soil by trampling for each treatment and habitat (kg/m^2) with confidence intervals

	Grassland		Heath		Mire		Woodland	
Treatment	C	T	C	T	C	T	C	T
Mean	1.96	2.14	0.37	1.27	1.16	1.29	0.98	1.29
C.I.	0.36	0.37	0.14	0.18	0.12	0.18	0.18	0.18

Regression analyses for trampling intensity and soil compaction for each habitat however did not reveal any significant causal relationships between trampling and soil compaction (Grassland: B=-0.011, *R-squared* =0.001, F=0.086, *P*=0.771, intercept=2.158, *t*=7.028.

P<0.001; Heath: B=0.006, *R-squared* =0.004, F=0.208, *P*=0.650, intercept=0.320, *t*=2.934. *P*=0.005; Mire: B=-0.007, *R-squared* =0.003, F=0.149, *P*=0.701, intercept=1.334, *t*=9.145. *P*<0.001; Woodland: B= -0.005, *R-squared* =0.001, F=0.038, *P*=0.847, intercept=1.318, *t*=7.523, *P*<0.001). The slopes of each regression did not indicate any causal relationships and minimal variation in compaction was explained by trampling intensity according to the *R*-squared values (Appendix 11).

Table 5.10: *F*-statistics from two-way analysis of variance for soil compaction treatments across habitats for all trampling plots

Between-subject effects	*d.f.*	*F*	*P*
Treatment	1	1.125	0.289
Habitat	3	22.269	0.000
Treatment x Habitat	3	37.762	0.000

5.4. Discussion

5.4.1. Shaping vegetation communities

The changes in plant composition in this study demonstrated that natural trampling played a role in shaping vegetation communities on the lowland heath system. It was clear from the experimental design that the effect of herbage removal could not be exclusively removed from the trampling impacts measured, but trampling was the primary mechanism determining impacting the vegetation as the plots were in transient areas. Recording the natural impact of herbivores through these mechanisms is a novel approach on lowland heath.

Overall the trampling effects to vegetation communities were not as distinct as herbage removal (Chapter 4), demonstrating that these mechanisms were largely separate, but there was a modification to some plant groups in the community, such as graminoids (Fig. 5.3) (Table 5.2). The non-trampled treatment allowed graminoids to expand within these areas, owing to their rapid capacity for growth and colonisation (Striker et al., 2011), especially on heath systems (Mitchell et al., 2008). The relative proportion of graminoids remained high on trampled areas, around half of all the species again supporting the minimal herbage removal occurring. Stem flexibility in graminoids also meant minimal damage was incurred which was important for tolerating trampling (Sun and Liddle, 1993), a contributing factor for physical architecture. For graminoids, low-density trampling modified the plant composition, answering part of research question (i) (*sub-section 5.1.6*).

The presence of key species in the habitats, such as *Myrica* and *Calluna* in mire and heath, contributed to the significant difference in the functional group composition of woody plants between the habitats. These key species also contributed towards the significant interaction effect observed (Table 5.2). The woody plants were susceptible to physical damage by trampling and were slow to regenerate subsequently (MacDonald, 1990, Bokdam, 2001). Their comparative abundance remained unchanged however (Fig 5.3), and displayed by the similar abundance in trampled and non-trampled treatments, according to the ordination plots and non-significant difference. The minimal differences in plant community in heath may be due to *Calluna vulgaris* which forms a closed canopy prior to reaching the late mature stage and discourages other plant species from invading

(Britton et al., 2000a). In terms of species composition only recorded the presence of individual plants and not their morphological state (i.e. if damaged but still in situ), which could also offer a reason for the unchanging abundance. In addition structure measured the vegetation as whole and not individual plants, so this was not a suitable measure when examined in accordance with species composition. The remaining functional groups were also not observed to vary according to the trampling. For example, other plants (e.g. bryophytes) were not present in high numbers and forbs did not vary markedly due to their low stature (Kobayashi et al., 1997). Forbs and other plants responded differently due to habitat (Table 5.2), owing to the high abundance in grassland and woodland respectively and are often variable due to site characteristics such as stocking level (Bullock and Pakeman, 1997).

If there was a change to the vegetation community, it was not presented by assessment of the selected key species as differing effects were not displayed, so at a species level the composition was not modified by trampling as it was for herbage removal (Chapter 4). *Agrostis* was dominant across all habitats and treatments (Fig. 5.4), indicating its competitive ability in persisting despite disturbance (Wilson et al., 1996, Hartley and Mitchell, 2005) and displaying the absence of herbage removal in these plots as this species is likely to have been removed if herbage removal was occurring. Other graminoids, including *Molinia, Festuca and Carex*, were also widespread but did not show significant differences between trampling treatments (Table 5.3). As reported in other heathland studies, stocking density and nutrient levels are critical in dictating the competitive balance of such grasses (Hartley and Mitchell, 2005) and the low-density mixed regime was an important determinant. It can also be suggested that the plant tolerance to changing canopy conditions increased their longevity in most habitats (Welch and Scott, 1995) as was clearly evident here by their ubiquity across the system. Additionally, the change to the vegetation community was also reliant on the changes to spatial cover and the way the plants respond in the horizontal plane following trampling. This response was clearly shown by herbage removal and may be true of trampling, discussed later.

Based on the dominance and changing abundances of graminoids, decisions about their management require careful consideration of trampling pressure. Low stocking density had a moderate trampling pressure in the sampled areas and controlled graminoid dominance. This low pressure was likely to be important for generating more sites for establishment especially for slow-growing ericaceous plants (Mitchell et al., 2008). An increase in pressure is likely to result in heavy poaching and consequently a decline in desired species such as *Calluna*, with an increase in invasives such as *Molinia,* as seen in upland moorland (Welch and Scott, 1995, Critchley et al., 2008); but this was not assessed here. Hester and Baille (1998) did note however that even at low densities, similar to those in this study, the impact of trampling on heather was damaging and became critical as herbivore densities reached a threshold before grazing became more contributing (Hester and Baillie, 1998). Natural trampling and grazing were recorded together in Hester and Baille's study, as they were in this study, indicating their relatedness and the difficulty in separating their effects under natural field conditions. Nevertheless, in other studies low-stocking densities have had differential trampling effects on vegetation, where patch distribution and size were more important (Oom et al., 2008), although in spatial assessments of vegetation impacts the patch characteristics can also be influential. Differences in *Calluna* abundance were not significant due to trampling in the study undertaken here (Table 5.3), indicating that the decline due to intensive trampling seen on moorland (Welch and Scott, 1995) was not a problem on a minimally-stocked system such as at Eelmoor. It may also have been the lower intensities were not severe enough to break the woody branching stems, which are often brittle in mature heather and suffer damage from trampling (Gimingham, 1972, Palmer and Hester, 2000). A changing community composition, particularly for reducing graminoids, favours the grazing regime in this study and for lowland heath conservation.

5.4.2. Physical effects on vegetation

The effect on spatial and structural parameters between trampled and non-trampled vegetation was displayed by the direct impact that trampling had on the lowland heath system. The study supported the wealth of work that has documented animal trampling as a key mechanism in altering vegetation architecture, across different vegetation types (Mitchell and Kirby, 1990, Cole, 1995a, Kohler, 2004). The work carried out on upland heath by Mitchell et al. (2008) was of particular importance because of its applicability to the study system. This work recognised that trampling intensity on *Calluna* establishment is an important factor for the restoration of conserved habitats, primarily due to the creation of bare open ground (Mitchell et al., 2008).

The exclusion of herbivores from areas resulted in a significant response in sward height, as would be expected (Fig. 5.5). The increase was observed across all habitats but was most marked in grassland and mire, which was attributed to the net primary productivity (NPP) of the communities and their plant composition, e.g. graminoid abundance (Milchunas and Lauenroth, 1993, Begon et al., 1996). The minimal difference observed between woodland treatments supported this explanation (Fig. 5.5), as did the soil chemical properties observed for these habitats (e.g. acidity and available P) (Appendix 4). Despite the presence of graminoids in both trampled and non-trampled grassland plots, the sward differed due to their ability to rapidly grow in non-trampled areas and persist with a reduced prostrate morphology in the trampled areas (Cole, 1995b, Striker et al., 2011). In balance, there could have been an influence of herbage removal here, especially on these selected habitats (Chapter 3), but was unlikely to have been the primary factor for change owing to the positioning in transient areas and the camera trapping data. In contrast, woody plants were only largely abundant in mire, such as *Myrica gale* which relies heavily on acidic wet soil and has woody rhizomes and branches (Skene et al., 2000), which because of an inferior ability to regenerate quickly after trampling damage in comparison to monocots (Hobbs and Gimingham, 1987) resulted in a significant difference between treatments. In addition, *Myrica gale* has the potential to alter the surrounding vegetation due to it nitrogen-fixing capability (Skene et al., 2000) which could have resulted in its high abundance with grasses in the non-trampled areas. Overall, canopy or sward height was therefore modified with trampling (Table 5.4), answering part of the second question posed within this study. This parameter was also related to the structural complexity as seen in other systems (Schwab et al., 2002).

Low trampling density allowed a richer and more diverse sward to be developed at the patch scale, created by low to moderate disturbance (Evans et al., 2006, Marion et al., 2010), but a higher degree of structural heterogeneity was observed on non-trampled vegetation (Fig. 5.6 and Table 5.5). The documented increase in structural complexity by low-level trampling reported elsewhere (Olff and Ritchie, 1998, Pavlu et al., 2007) was not recorded. The structure of the vegetation was modified, answering this part of the second research question (*sub-section 5.1.6*), but was opposite to the expected effect that trampling would enhance structural heterogeneity of the habitat (Dennis, 1998). The corresponding increase in sward height with structural intercepts resulted in an increased canopy density, which is likely to have contributed to the effect, observed in tall angiosperm species in grassland (Schwab et al., 2002). This was a similar effect discussed in Chapter 4 for herbage removal and indeed this mechanism could have played a role, despite the control of this factor by the experimenter. In addition, the significant interaction term demonstrated that structure responded differently to trampling with each habitat (Table 5.5), although a large sample means this was concluded with caution. Finally, the type of vegetation and the plant attributes within each habitat determined the degree of resistance, tolerance and resilience to trampling (Cole, 1995b) and therefore the structure. Understanding the composition, structural characteristics and typical response of vegetation was valuable for determining the knock-on effects to invertebrate assemblages (Dennis, 1998), a subject of considerable importance for lowland heath management and an area in need of further investigation.

Monitoring changes to the spatial cover of plants were important measures of invasiveness, a widespread problem in lowland heath systems (Bokdam, 2001, Hartley and Mitchell, 2005) and a valuable measure for conservation management (Mitchell et al., 2008). The observed difference in grass cover (Table 5.7) across all habitats at the expense of herbs and woody plants on trampled areas (Fig. 5.7) is indicative of this invasiveness and the dominance of grasses (Augustine and McNaughton, 1998, Bokdam, 2001). The covariate, soil compaction, was not significant but likely reduced the error for the effect. Across all habitats there was a high proportion of grass cover, supported by the findings of a high composition of graminoids in all habitats. On grassland and woodland there was an increase in grass cover on the trampled areas and little change on heath and mire, but overall a significant difference for trampling. These findings meant that grass cover did not decrease with trampling and it was suggested that new sites created by trampling were being colonized by grasses, as seen in the other similar systems (Bokdam, 2001). In heath habitat specifically, the minimal change may be caused by the unfavourable conditions for grasses such as dense canopy and low nutrient availability (Hartley and Mitchell, 2005), although they remained within the community as seen in the compositional data. The findings meant that for lowland heath the invasiveness of grasses occurred in habitats already dominated by grasses and where new gaps could be easily colonized. The change in grass cover was not minimal like that seen in upland heath systems (Hartley and Mitchell, 2005), but nutrient availability was a factor and detailed examination of nutrient composition is of undoubted importance in this lowland heath.

An additive effect may have occurred with grass cover and gap cover (Fig. 5.8), where the gaps created were occupied by the opportunistic plants (Critchley et al., 2008). Persistent low level trampling continued to create additional gaps in the vegetation and as the susceptibility of invasion is strongly related to the availability of bare ground (Burke and Grime, 1996) grasses continued to colonise. The significant difference indicated that the non-trampled areas had a lower mean gap cover (Table 5.8) and therefore a more closed sward. This answered the second question that total plant cover was modified with trampling (*sub-section 5.1.6*), which is also supported by the sward height data and the increased canopy density argument (Schwab et al., 2002). As these areas change in their spatial heterogeneity over time further assessment will be needed to measure if they are long-term changes. Indeed investigation should consider if the composition of the sward is altered on a successional basis, i.e. whether it is over several years or just a year-on-year fluctuation in growth, removal or mortality (Bokdam, 2001). It is these assessments which will be crucial for protected reserve management, but the suite of vegetation parameters provided an effective tool for quantifying the impact.

5.4.3. Physical changes to the soil

Substrate effects were observed based upon trampling and as expected, the findings of the physical assessments of the soil structure displayed a higher compaction in the grassland areas (Table 5.9). This indicated that the soil properties were affected by the herbivores' movement to adjacent foraging habitat. The higher soil compaction values in trampled areas showed that the trampling did alter the soil's physical properties and was likely to be due to a breakdown in the soil structure (Britton et al., 2005), satisfying the third question set out (*sub-section 5.1.6*). The significant interaction for trampling and habitats (Table 5.10), corroborated with the differing soil profiles between these habitats (Allen, 1999)(Appendix 4), different occupancy (Chapter 3) and differences in plant resistance (Crawford and Liddle, 1977). Soil compaction would be expected to impact the vegetation parameters across the habitats, typical of degradation of the soil profile by an increase in soil bulk density and decrease in air permeability (Mitchell and Kirby, 1990, Whalley et al., 1995). The grass cover parameter indicated that this was not the case and was not a significant covariate of change to spatial heterogeneity; although comparison with structure may have perhaps been a better assessment as it would have better indicated plant resistance (i.e. following damage). Regrettably, this analysis was not possible due to different sample sizes, but further work on this should be undertaken.

The change in the soil structure or compaction as a result of trampling intensity was not supported by the regression analysis. This result, and those of grass cover, may have been due to the low-level and heterogeneous impact that natural trampling had on the substrate or even the resistance of some areas to trampling (Kohler et al., 2006b). This heterogeneity is valuable for maintaining a variable sward. The significant difference between trampled and non-trampled areas and the increase in architectural parameters in non-trampled areas are likely to be related as observed in other studies of soil hardness and porosity (Kobayashi et al., 1997). The reduced sward and structural heterogeneity, affected by physical damage in the first instance, may be attributed to degradation of the soil which is likely to alter the vigour of the vegetation, its capacity to recycle nutrients and soil structure, as it has on other substrates (Nicking and Wolfe, 1994, Kobayashi et al., 1997, Hiernaux et al., 1999). Care must be taken, however, to understand if these are plant adaptations, such as low-growing morphological traits. It was regrettable that analysis could not be undertaken between vegetation structure and soil compaction.

The increase in gap cover in trampled areas may have supported the explanation of reduced vigour in compacted soil, but further study is required. There have also been effects noted in the quality of litter accumulation following changes in vegetation due to trampling (Kohler et al., 2005), which have lead to effects on the regenerating vegetation. This effect was shown in the difference in woody plant composition. The main differences observed were in heath and mire habitats which have a high level of litter accumulation (H, F, L horizons) and are susceptible to physical damage by trampling (Fig. 5.3) (Table 5.2).

5.4.4. Evaluation and limitations

The impact of trampling within this chapter was difficult to isolate from the herbage removal mechanism, although this was best achieved by the methods outlined in section 5.2. In order to directly inform the habitat management, trampled areas did not exclude herbage removal or dunging, to maintain the effect of actual non-simulated trampling which although documented in other systems has not been experimentally achieved in lowland heath previously. Negligible grazing and dunging was recorded from camera trapping data in these transient areas (camera-trapping data), selected specifically for this reason from the habitat occupancy and selection data in Chapter 3. Nonetheless, as the affects of herbage removal and dunging were not completely controlled for within the design, they should be accounted for in any explicit recommendations for those relating to trampling. For example when creating spatial heterogeneity in the sward in tandem with herbage removal by both horses and cattle (see *sub-section 5.4.5*).

With regard to the methods used to record vegetation parameters it was possible that the structural sampling method may not have been directly comparable between habitats because of the differences in vegetation structure. A suite of structural measures should be incorporated, initially recorded at the vegetation sampling stage but not utilised due to research constraints, following the methods of Schwab et al. (2002). This study assessed a number of structural parameters of hay meadows and described how these parameters can be used as surrogates to estimate ecological diversity, although these were only directly comparable to the grassland in this study (Schwab et al., 2002). The detailed records in this research were able to quantify the structural change however which again was novel against the backdrop of other research quantifying trampling, tending to only make broad assessments of vegetation change (Cole, 1995a, Kobayashi et al., 1997). It was possible that the short-term examination of trampling effects meant only an early stage of vegetation response was observed. A suite of measures such as Schwab et al. (2002) may have been more suited for the more productive grasslands (macro-nutrient levels, Appendix 4), but not for the woody plant dominated heath and mire; therefore a broader comparator remains best suited. The work by Schwab et al (2002) was central for quantifying the changes to habitat structure and would be valuable for assessing the impact on invertebrate communities (Cluzeau et al., 1992, Gibson et al., 1992, Dennis, 1998) which can be investigated in the future.

Upon evaluation it is clear that trampling impacts vegetation in a number of different ways, and the findings indicated that some parameters are highly associated, for instance sward height and structure being the most influenced by trampling. The results of structural heterogeneity showed that canopy density is important which was not foreseen.

The importance of these two parameters is documented in a number of studies (Schwab et al., 2002, Stewart and Pullin, 2008) and the benefit of understanding these for monitoring lowland heath communities is hugely valuable.

Finally, the compaction of the soil had negative effects by reducing vegetation parameters which may have also been attributed to productivity, although it did indicate that soil compaction was not a significant covariate of grass cover (Table 5.7). Further soil compaction assessments may be appropriate, such as bulk density or shear strength of soil (Bachmann et al., 2006). Indeed, spatial heterogeneity measures also indicated that the creation of gaps was likely to provide niches for invasive plants to occupy and dominate, but extending the work would benefit.

5.4.5. Implications for management

The findings support the work of other studies indicating the importance of trampling in the maintenance and enhancement of vegetation communities (Albon et al., 2007, Mitchell et al., 2008). The work also provided an approach to quantify the impact of mixed low-level trampling. The trampling disturbance, achieved at low stocking densities, opened sites for germination, diversified the sward to enhance the ecological value of the habitat but had minimal effect on the overall species composition, an important factor to understand for heathland management.

Several specific recommendations, based on this study, can be made for trampling on lowland heath:

- Trampling can be utilised to regulate graminoid abundance, but lateral growth is likely;
- Woody plants can be limited by trampling, especially on mire, to aid the prevention of scrub invasion (damage to desired dwarf-shrubs, e.g. *Calluna,* was not observed)
- Horses and cattle together should be used to create spatial heterogeneity in the sward and trampling, with herbage removal, can reduce grass cover and increase gap cover;

- Trampling at low-stocking densities in mixed regimes can be employed to modify dense vegetation in need of management and reduce architecture (sward, structure) generating a heterogeneous sward;
- Trampling, in this study, even at the density of ~0.20LU/ha caused significant differences in soil compaction, so should be employed with care to avoid soil degradation. However in a diverse habitat system the differential occupancy will have heterogeneous effects.

The natural trampling by horses and cattle, within the four broad habitat types, and their impact to the vegetation showed the complex dynamic of interactions which must be quantified to inform conservation management of these systems, addressing research objectives 2 and 3 (section *1.11*). Trampling is important for governing vegetation communities, as some of the particular effects to vegetation are comparable with herbage removal, while other effects are individual. Quantifying this impact mechanism separately has comprehensively and innovatively addressed its influences and revealed underlying processes, all of which are valuable for informing managers.

The two physical impact mechanisms to vegetation have been quantified in this thesis so far, but equally important is the indirect impacts of dunging or nutrient input. The following chapter quantified the relative effects to vegetation by dunging, which will complete examination of the complex of mechanisms of large herbivores in this thesis.

Chapter 6

The impacts of herbivore dunging and nutrient input on lowland heath

Summary

An increase in nutrient availability results in biological and architectural changes in a heterogeneous plant community. Graminaceous plants dominate under increasing fertility conditions, altering the vegetation characteristics in nutrient-poor systems like heathland. The absence of experimental assessment of dunging impacts and regime (e.g. animal, worming regime) on lowland heath vegetation is apparent. The study seeks to quantify the impacts by asking (i) does dunging regime affect the plant community composition? (ii) Is sward height increased in response to dung application and what is the effect of the regime? (iii) Does dunging regime govern structural and spatial heterogeneity in each habitat? And (iv) is there an effect of soil chemical properties on spatial heterogeneity and are there related impacts of regime on the spatial heterogeneity of the vegetation?

An assessment of dunging effects (horse and cattle, wormed and non-wormed, dunged and non-dunged) on the vegetation communities across four habitat types (grassland, heath, mire and woodland) was carried out in experimental simulated field plots. Vegetation parameters were recorded and evaluated changes to composition, sward height, structure, spatial cover and soil chemical properties in each sub-plot over a three year period. Analyses were carried out using general and generalized linear models for factors: animal, worming, treatment.

Nutrient availability was influential on species composition for graminoids, sward height in all habitats particularly mire and structure in grassland. Worming effects were evident in mire for sward, while animal and worming differences were evident in plant composition of graminoids in grassland. Plant composition was also altered by the same effects for *Agrostis* and *Molinia* in grassland, and for grass cover in woodland, owing to delayed dung degradation and animal dung properties.

The effects of the main factors (animal, worming, treatment) determined changes to vegetation community and architecture. The observed effects were critical for making management decisions, such as removing or reducing density of cattle during key vegetation growth periods or returning to traditional overnight stabling practices. Implementing animal-specific dunging regimes can also benefit the overall nature conservation for the control of dominating plants in such vulnerable heathlands.

6.1. Introduction

6.1.1. Dunging and vegetation change

Recurrent nutrient inputs can have marked effects in altering the local nutrient balance (Gough et al., 2000, Kohler et al., 2004) and the competitive balance between plants (Crawley, 1983), modifying the overall plant community composition. For example as nutrient levels increase a positive growth response is observed in some plants but there may also be a suppression of others (Hartley et al., 2003, Pywell et al., 2007). Micro-scale changes in the vegetation due to dung input can alter species richness (Dai, 2000, Augustine and Frank, 2001) and have localised effects on diversity through spatial heterogeneity (Olff and Ritchie, 1998). A widespread increase in soil fertility, however, is largely unfavourable for the plant community by promoting nitrophilous species (Kohler et al., 2004) and increasing aboveground biomass which destabilises the plant community (Hobbs, 1996). The heterogeneous nature of free-ranging herbivore dunging means the impact to vegetation communities and the response of individual plants can be temporally complex and spatially variable (Hartley and Mitchell, 2005).

Individual plant responses to dunging can be broadly classified based on their life history traits, such as the swift uptake of macronutrients (e.g. available nitrogen) by graminaceous plants for rapid utilisation in growth (Jørgensen and Jensen, 1997, Gillet et al., 2010). These plants are capable of dominating the sward and outcompeting slower-growing herbaceous plants which respond less readily to a change in nutrient availability (Bokdam, 2001). In contrast, woodier shrubs may develop new growth based on the addition of nutrients, although in the long term unfavourable substrate conditions can be developed enhancing grass dominance (Hartley and Mitchell, 2005). The particular traits of the plants and the plant community are important for understanding the structural and compositional changes that are brought about by dunging. Such structural traits include sward height which is increased through increased biomass, particularly for invasive graminoids (Williams and Haynes, 1995). This is observed in many systems with a high propensity for successional change, such as heathland, especially following the cessation of management (Gimingham, 1972, Barker et al., 2004, Critchley et al., 2008).

6.1.2. Heathland systems

Among the responses of vegetation communities to dunging, agricultural function has been extensively studied in terms of productivity (Williams and Haynes, 1995, Powell et al., 1998) as well as changes to community composition at pasture (Kohler et al., 2004, Gillet et al., 2010). Studies that experimentally evaluate the impact within natural or semi-natural areas such as heathland are scarce (Bakker et al., 1983, Britton et al., 2005). The fragile status of heathland plant communities, which by their nature are in a state of sub-climax succession, means they are susceptible to change though nutrient enrichment (Gimingham, 1972). Heathland ecosystems have been maintained at a low-nutrient level through human-related activities (Webb, 1986, Price, 2003), once achieved by the cutting of turves, vegetation removal for animal fodder and extensive grazing practices which were commonplace prior to modern agriculture (Webb, 1998). These activities created a highly acidic low fertility substrate and although relatively less diverse than, for example, calcareous grassland, acid oligotrophic heath is rich in vascular plants (Gimingham, 1972). The distinctive communities were widespread until around 1750 when the loss of active management, abandonment and the ease of cultivation of poorer soils became more commonplace (Price, 2003). Abandonment generated favourable conditions for change in the vegetation communities and left a fragile system predisposed to rapid succession by invasives (Bullock and Pakeman, 1997).

Dunging on heathland can provide a favourable environment for invasives, colonised readily by opportunistic and fast-growing plants such as grasses (*Agrostis* sp. and *Deschampsia* sp.) and nitrophilous bracken (*Pteridium aquifolium*) (Gimingham, 1972, Manning et al., 2004). These successional processes can be detrimental on remnant heath through continual degradation and cause long-term loss of heathland habitat (Mitchell et al., 1997). A lack of investigation of these dunging effects, specifically the impacts on botanical communities on lowland heath, is demonstrated in the literature; only broadly reviewed as part of wider management (Bullock and Pakeman, 1997, Lake et al., 2001, Newton et al., 2009). Studies focussing on montane heather communities in Wales (Britton et al., 2005), upland moorland in the north of England and Scotland (Welch and Scott, 1995, Hartley and Mitchell, 2005) and across continental Europe (Aerts and Berendse, 1988, Borghesio et al., 1999) have similarities with this research, but there are differences in vegetation community and structure. These differences are important attributes for understanding the impacts of large herbivores and for the conservation management on lowland heath.

6.1.3. Herbivore dunging regime

The review of management of lowland heath by Bullock and Pakeman (1997) considered the differences brought about by mixed herbivore regimes, especially between horses and cattle. The regime is a major factor generating community change and different grazers have diverse effects through dunging behaviour, leading to differential nutrient and seed transfer between communities (Lake et al., 2001, Cosyns et al., 2005). The differences in activity documented in Chapter 3 are likely to lead to plant community variation. This variation may be due to dunging intensity and behaviour (Edwards and Hollis, 1982), digestive physiology (Sneddon and Argenzio, 1998), respective nutrient extraction (Lamoot et al., 2005) as well as the effects of parasitic treatments (antihelmintics) on dung degradation and nutrient availability (Sommer and Bibby, 2002, Iglesias et al., 2006, Bloor et al., 2012). In order to implement effective herbivore management on lowland heath, the effects of these dunging regimes on vegetation must first be quantified. This has been recognised in a heathland study in the Netherlands on short-term vegetation change (Bokdam and Gleichman, 2000), and documents that management should incorporate animal type, intensity and parasitic medications for example. Vegetation monitoring on heath can inform specific management prescriptions (Bakker et al., 1983, Canals and Sebastia, 2002) and provide information on the ecological processes driven by herbivore dunging.

The assessment of dunging effects on broad habitats of a lowland heath system is also valuable because of the varying vegetation successional state (Bokdam, 2001), relative occupancy (Chapter 3) and vegetation or soil differences (Grant and Armstrong, 1993, Mitchell et al., 1999, Bloor et al., 2012). The characteristics of these habitats, some of which are communities confined to the British Isles (Price, 2003) and some comparable to other heath systems on continental Europe (Bokdam and Gleichman, 2000, Vandvik et al., 2005, Celaya et al., 2010), provide a unique research opportunity. This chapter assesses the effects of dunging regime on the different vegetation communities within a lowland heath system, with specific comparison between horse and cattle dunging and worming regime.

6.1.4. Quantifying the effects of dunging

In a lowland heathland system, an experimental manipulation of large herbivore dunging was undertaken using fenced exclosures and four dunging applications across four broad habitat types (open grassland, heath, *Molinia*-dominated mire and secondary woodland), measuring the effects on the vegetation communities both in terms of architecture and plant composition.

The general aim was to quantify the effects of dunging regime on vegetation in the lowland heath system to make recommendations for grazing management on natural or semi-natural areas, addressing overall research objectives 2 and 3 (section *1.11*). Specifically, the chapter assesses a number of research questions:

(i) Does dunging regime affect the plant community composition?
(ii) Is sward height increased in response to dung application and what is the effect of the dunging regime?
(iii) Does dunging regime govern structural and spatial heterogeneity in each habitat?
(iv) Is there an effect of the soil chemical properties on spatial heterogeneity and are there related impacts of dunging regime on the spatial heterogeneity of the vegetation?

6.2. Methods

6.2.1. Study site and animals

The study was conducted at the Eelmoor Marsh Site of Special Scientific Interest, Hampshire, UK. The study site is described fully in Chapter 2 General Methods which outlines the statutory designations, broad habitat types and vegetation communities, among other site characteristics. Particular attributes that are of importance for this chapter will be described in more detail here.

The site was stocked with ten Scottish Highland cattle (*Bos taurus*) and six Przewalski's horses (*Equus ferus przewalskii*) at stocking densities of 0.12 and 0.08 livestock units per hectare (LU/ha) (cattle and horses, respectively) across the entire site. Veterinary interventions were only carried out when required. The animals were not treated with antihelmintic (worming) medications, but monitored for body condition with faecal screening undertaken at regular intervals; according to recommended conservation grazing practices (Tolhurst, 2001).

6.2.2. Experimental design

A balanced factorial design was established in the four broad habitats (grassland, heath, mire, woodland). The design was a comparative examination of horse and cattle dunging (with worming factor) on the vegetation communities within the broad habitat types. The dunging plots differed from the herbage removal (Chapter 4) and trampling (Chapter 5) plots as they assessed simulated impacts on the habitat. Three replicate blocks were located in each habitat, fenced May 2008 to September 2011, excluding both grazers. Each block was 79.5m^2 and rectangular in shape to incorporate all factors and their sub-plots. The blocks excluded herbivores, but roe deer (*Capreolus capreolus*) and rabbits (*Oryctolagus cuniculus*) were not excluded as they had minimal presence, based on field observations. Exclosures were constructed from untreated spiked timber posts with two wire bands and were parallel to a south-orientation to equalise the sunlight and dung (and worming medication) degradation effects (Halley et al., 1989, Kohler et al., 2005).

Four 2×4 grids of treatment combinations formed the factorial design (Fig. 6.1). Wormed treatment denoted application of dung from wormed stock and natural treatment from non-wormed stock. Each 1m^2 plot was surrounded by a 0.4 m buffer strip to minimise the spread of nutrients and edge effects (Kohler et al., 2005). A 1 metre wide buffer zone divided the natural treatments (non-wormed), wormed and between animal treatments. Controls provided a non-dunged comparator for the respective treatment combination; no faecal matter was applied to these plots. Wormed control and natural control plots were equal apart from position, included for demonstration purposes. An analysis was undertaken to test for differences and these plots were equal for vegetation change. A grid design was favoured over using separate larger experimental plots (Kohler et al., 2004) because of logistical constraints.

Faecal matter was collected and diluted according to the dunging intensity based on a preliminary assessment. The volume of water was kept to a standard minimum to mitigate increased soil moisture. Non-wormed dung was collected from the study site, while wormed dung from domestic Highland cattle (*Bos taurus*) was collected from animals kept on similar habitat and wormed dung from Przewalski's horses (*Equus ferus przewalskii*) from Marwell Wildlife, Hampshire. The assessment of dunging intensity was carried out by collection of preliminary data on the frequency and mass of defecations from fourteen 30m^2 plots for each animal (Bakker et al., 1983, Kohler et al., 2006b). A two sample Kolmogorov-Smirnov test assessed the null hypothesis that the two animals had equal frequency distributions and aggregation of defecations. Comparative dunging intensity (CDI) was also calculated to assess aggregative behaviour, according to the formula (Bakker et al., 1983):

$$\mathrm{CDI} = \frac{A}{a} \times \frac{\mathrm{d}(t_2 - t_1)}{D2(t_2 - t_1)} - 1$$

where A = entire study area (m^2); a = sampled area in section a (m^2); d = amount of dung in the sampled area in a (ml) accumulated over the period (t_2 - t_1); D = amount of dung in the entire study area (ml) accumulated over the period (t_2 - t_1).

Based on the dunging intensity and the methods by Kohler's et al. (2004, 2005), faecal input was calculated for each animal: (horse: 0.70 kg m^{-2}; cattle: 0.45 kg m^{-2}), spread homogeneously across the 1m^2 plots repeated every two months on the same day and time for 24 months to avoid any seasonal-temporal variation (Kohler *et al.*, 2005) mirroring year-round presence of herbivores.

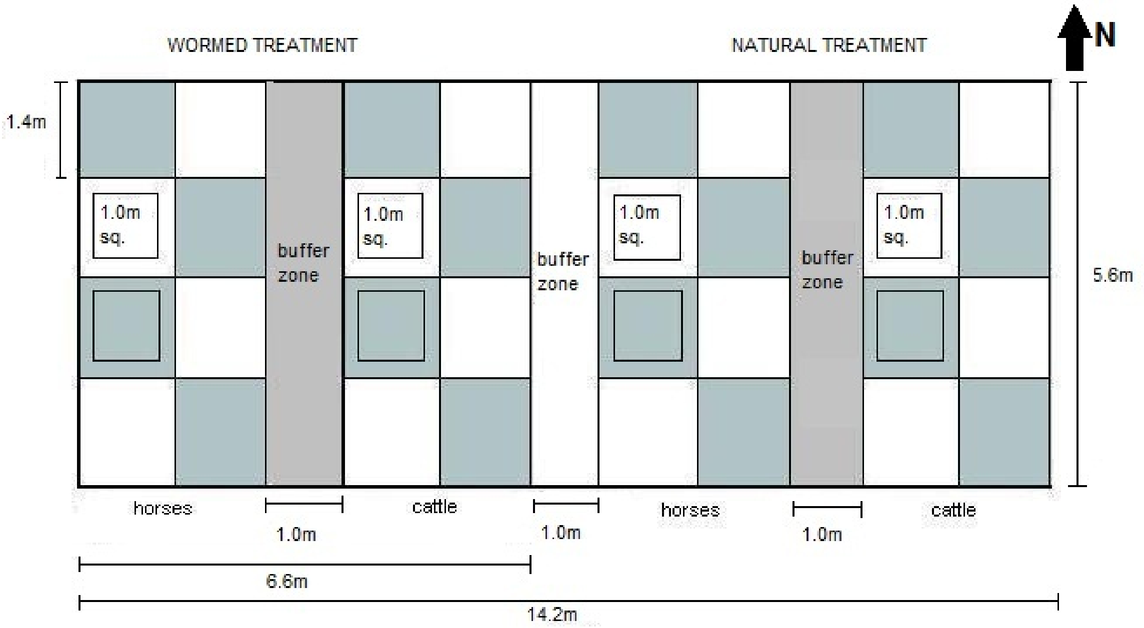


Figure 6.1: Experimental exclosure for dunging and control treatments of horses and cattle. Natural treatment denotes the experimental design for this chapter. Sampling is taken from 1.0m^2 sub-plots within the 1.4m^2 plots (Treated areas = shaded squares; Controls = Empty squares).

6.2.3. Vegetation and soil sampling

The vegetation parameters measured in this chapter were approximately the same as those used in Chapter 4 (herbage removal) and Chapter 5 (trampling), although some specific parameters were measured for each. The standard parameters constituted a measure of the species composition (plant functional group, key species), sward height, plant structure and spatial heterogeneity (grass cover) of the vegetation. The vegetation parameters were measured within the dominant growth phases between May and August. All vegetation records were made in the central 1m^2 sub-plots. The vegetation parameter data sheet is shown in Appendix 5.

Species assemblages

Plant composition was measured using point-intercept frequency measurements (Buttler, 1992). Methods described in Chapter 2. Key species were *Agrostis, Juncus, Molinia, Carex* and *Calluna.*

Sward height

Sward height was measured (e.g. canopy height) eight times from within each sub-plot. Methods described in Chapter 2.

Structural heterogeneity

Structural heterogeneity and species composition of vascular plants was assessed using point-intercept frequency measurements (Buttler, 1992). Methods described in Chapter 2.

Spatial heterogeneity

The measure of spatial heterogeneity in the horizontal plane were measured based on the methods detailed in Chapter 2. Percentage grass cover was the primary measure.

Soil sampling

Soil sampling from each treatment sub-plot was taken after 24 months to assess dunging on soil chemical properties, on the same day to eliminate any effect of temporal variation. A macronutrient field testing kit was used for preliminary testing of macronutrient composition (potassium, phosphorus and magnesium and pH). Laboratory analyses were undertaken for a more accurate assessment of macronutrients using the same sub-plots, initially four samples from just one replicate of each habitat (Appendix 4). Soil samples of 350g were sent to NRM Ltd, Berkshire, for available phosphorus (mg/l), available potassium (mg/l), available magnesium (mg/l), total nitrogen (% w/w), organic carbon (% w/w) and pH. Comparison with the field test data deemed it necessary to send all samples for laboratory macronutrient testing (available phosphorus (mg/l), available potassium (mg/l), available magnesium (mg/l) and pH); nitrogen and carbon were not tested due to experimental limitations.

6.2.4. Statistical Analysis

Plant species composition for treatment and habitat effects was explored using cluster analysis and non-metric multidimensional scaling (NMDS) from the count data of plant composition of each sample plots. Following cluster analysis a SIMPROF (Similarity Profile) test was performed which created a mean profile after a number of permutations and then compared the data points to this profile to assess similarity (Clarke and Warwick, 2001) (see glossary). Count data were initially collected by species for plant species composition and then grouped into functional groups for analysis based on the same groups in Chapter 4, based on assessment of diet (graminoids - grasses, sedges, rushes, forbs - all herbaceous dicotyledonous species, woody plants, other plants - including mosses, lichens and ferns). The effects of dunging regime on functional groups were assessed using a three-way analysis of variance (animal × treatment × worming regime) within each habitat following arcsine transformation of proportions. Statistical analysis was not undertaken on the ordination data using ANOSIM (Analysis of Similarity, PRIMER) as the habitat assemblages had already been classified as different habitats so the data were not suitable (Clarke and Warwick, 2001). For key species analysis of variance was performed (*Agrostis* sp., *Juncus* sp., *Molinia* sp., *Carex* sp. and *Calluna* sp.) using the same factors; arcsine transformed prior to analysis.

Habitats were analysed separately within this chapter based on a high similarity observed in the cluster analysis (Appendix 13) and the non-significant difference in plant abundance for three key species (one-way analysis of variance for *Agrostis* sp., *Molinia* sp. *and Calluna* sp. with Sidak I-J post hoc testing (Dytham, 2009)). Habitat was also not incorporated into the analyses as a four-way analysis of variance was deemed very difficult to interpret statistically, due to the multiple interactions, and is not readily supported by statistical packages (Dytham, 2009). Sward height data were analysed with three-way analysis of variance (animal × treatment × worming regime) after logarithmic and square-root transformation of positively skewed data. Structural heterogeneity was analysed using a Generalized Linear Model with Poisson distribution for each habitat as there was high positive skew in each of the datasets, due to the zero-inflated data. A Type III analysis with Poisson distribution and a loglinear link function was carried out testing the differences in structural heterogeneity based on the three main effects mentioned previously (Welsh et al., 1996). The Wald chi-square statistic was used for its statistical power with large samples (Yi and Wang, 2011). Spatial heterogeneity data, grass cover, were arcsine transformed prior to three-way analysis (animal × treatment × worming regime). Additionally, a linear regression assessed the relationships between the soil properties (phosphorus, potassium, magnesium and pH) and the dependent variable grass cover. The soil properties (i.e. macronutrient or pH) that explained a significant proportion of the grass cover were incorporated as covariates in an analysis of covariance for grass cover, analysing the same main factors assessed in this chapter.

6.3. Results

6.3.1. Natural intensity of dunging (preliminary findings)

Calculated mean values of natural dunging provided the required dung application amounts. The mean mass per experimental plot (horse: 0.70 kg m^{-2}; cattle: 0.45 kg m^{-2}) was attained from the defecation frequency and mass (Table 6.1). There was no significant difference in the frequency distributions of number of defecations between cattle and horses within the trial data (K-S: Z=1.323, P=0.060, d.f. =26). The mean number of defecations for cattle of 6.50 (SE ±0.75) and for horses 10.71 (SE ±0.93) suggested a higher density of horse dunging, indicative of their aggregative dunging behaviour; although the distributions were not significantly different. This was supported by the Comparative Dunging Index (CDI) values which were not markedly different.

Table 6.1: Natural dunging intensities recorded within trial plots for each animal (mass, number and cover of defecations; comparative dunging intensity (CDI) calculation).

CATTLE					HORSES				
Plot	Mean Mass (kg)	No. of defecations	Mean Cover (m^2)	CDI	Plot	Mean Mass (kg)	No. of defecations	Mean Cover (m^2)	CDI
1	1.95	9	0.09	0.31	1	1.62	13	0.06	0.14
2	2.21	8	0.15	0.32	2	1.79	9	0.09	-0.13
3	2.23	4	0.14	-0.33	3	1.82	11	0.06	0.09
4	2.11	7	0.07	0.10	4	1.81	14	0.04	0.37
5	1.82	11	0.09	0.49	5	1.84	8	0.08	-0.20
6	1.97	6	0.06	-0.12	6	1.69	8	0.09	-0.27
7	2.16	9	0.1	0.45	7	2.01	5	0.09	-0.45
8	2.12	5	0.14	-0.21	8	2.08	12	0.11	0.35
9	1.98	3	0.08	-0.56	9	1.65	18	0.08	0.61
10	2.12	7	0.15	0.11	10	2.11	11	0.06	-1.00
11	2.09	9	0.11	0.40	11	2.01	14	0.05	0.53
12	2.01	1	0.08	-0.85	12	2.10	9	0.05	0.03
13	2.11	8	0.05	0.26	13	1.98	6	0.03	-0.36
14	2.08	4	0.09	-0.38	14	1.97	12	0.04	0.28

6.3.2. Species composition

6.3.2.1. Habitat assemblages

A total of 53 plant genera were identified from within 384 sample quadrats for treatment, worming regime and animals in all habitats. Cluster analysis demonstrated that the four habitat types were very broadly defined into grassland, woodland with a marginal habitat of heath and mire; overlaid onto the two-dimensional ordination of all habitats (Figure 6.2) (three-dimensional ordination is shown in Appendix 14). The one-way analysis of variance (n=96) for the three key species abundances demonstrated a significant difference overall, but post-hoc tests revealed non-significant differences (*Agrostis*: overall F=63.676, P<0.001; mire-woodland: Sidak I-J=2.294, P=0.414) (*Molinia*: overall F=88.889, P<0.001; heath-mire: Sidak I-J=0.937, P=0.967) (*Calluna*: overall F=387.498, P<0.001; grassland-woodland: Sidak I-J=1.722, P=0.230). As there was no difference between some habitats, the factor ‘habitat’ was not included in any subsequent vegetation parameter analyses.

A SIMPROF test revealed that woodland significantly delineated from the other assemblages at 18.25% similarity, Pi= 5.35 (P<0.1%), with grassland separating from heath and mire at 22.17% similarity, Pi = 3.09 (P<0.1%). Mire and heath delineated at a higher similarity of 38.89%, Pi = 1.78 (P<0.1%). As there was significant overlap between mire and heath it was deemed necessary to undertake analyses within each habitat (Appendix 13 and 16). It was likely that the key plant species contributed to the fourteen delineations identified (Appendix 13) (Fig. 6.3). For example, woodland separated from the rest of the habitat types at the first node (18.25%) supported by the abundance of typical woodland taxa, such as *Pteridium.* The apparent overlap and degree of similarity between heath and mire habitats was supported by the dominance of *Calluna* and *Molinia* sp*.,* whilst the relative abundance of *Agrostis, Festuca and Molinia* supported the similarity of grassland with heath and mire.

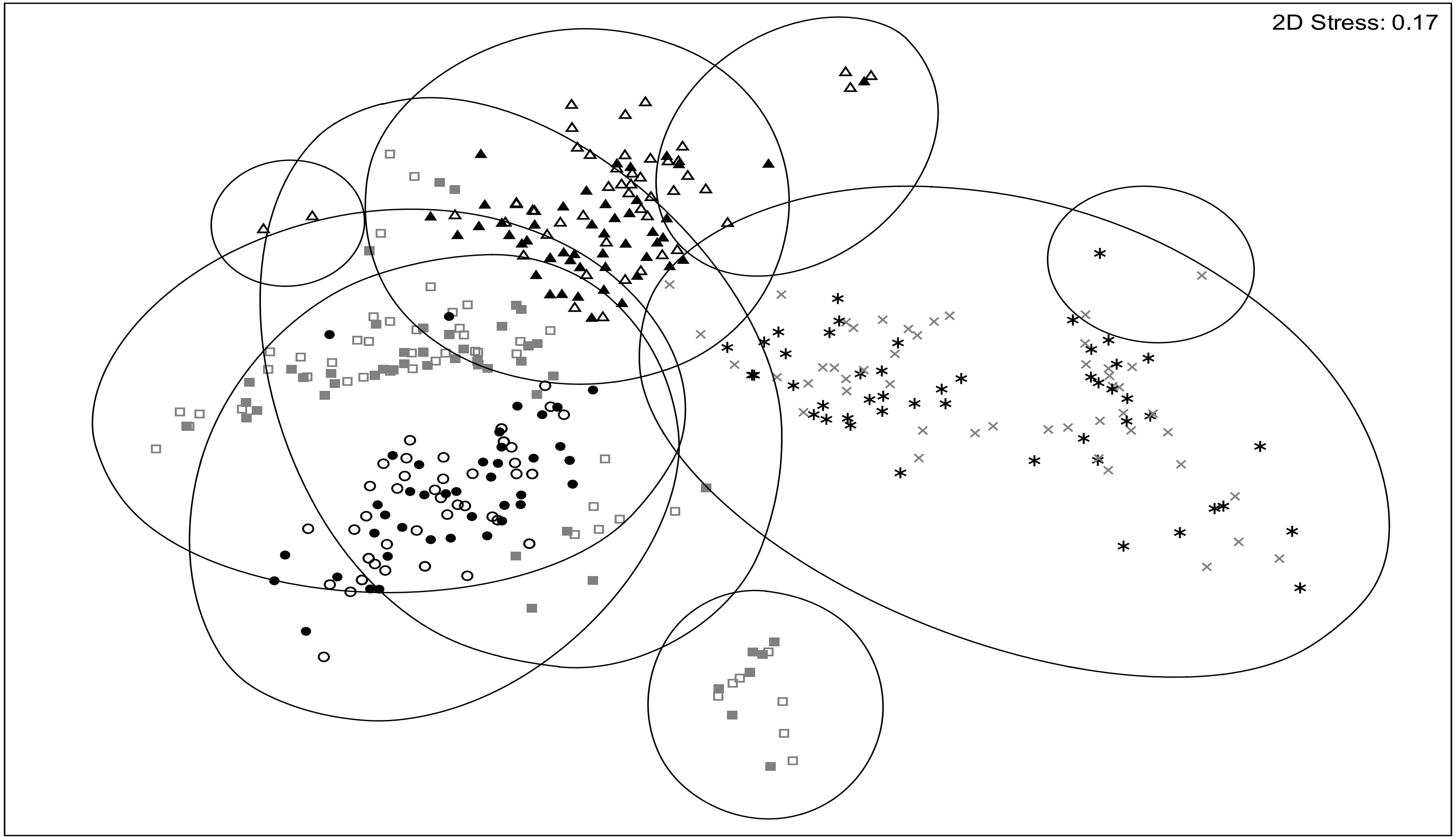


Figure 6.2: Two-dimensional non-metric multidimensional scaling for dunging habitat assemblages with 40% similarity contour . Δ Grassland Control, ▲Grassland Treatment, □ Heath Control, ■ Heath Treatment, ○ Mire Control, ● Mire Treatment, × Woodland Control, ✱ Woodland Treatment.

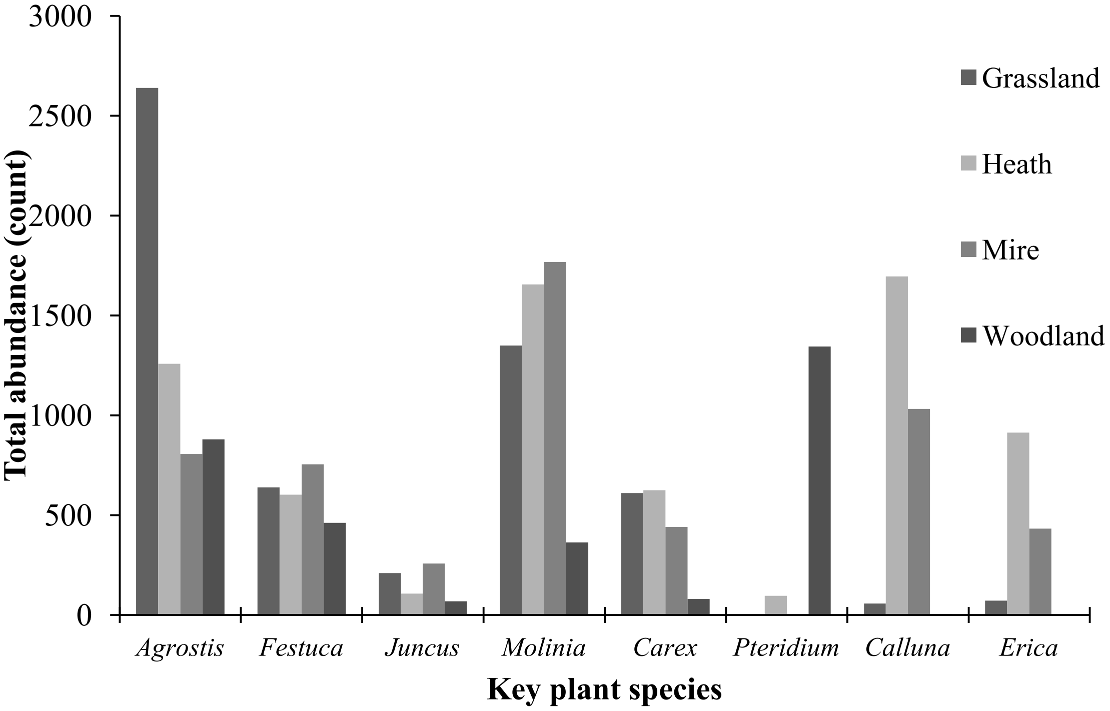
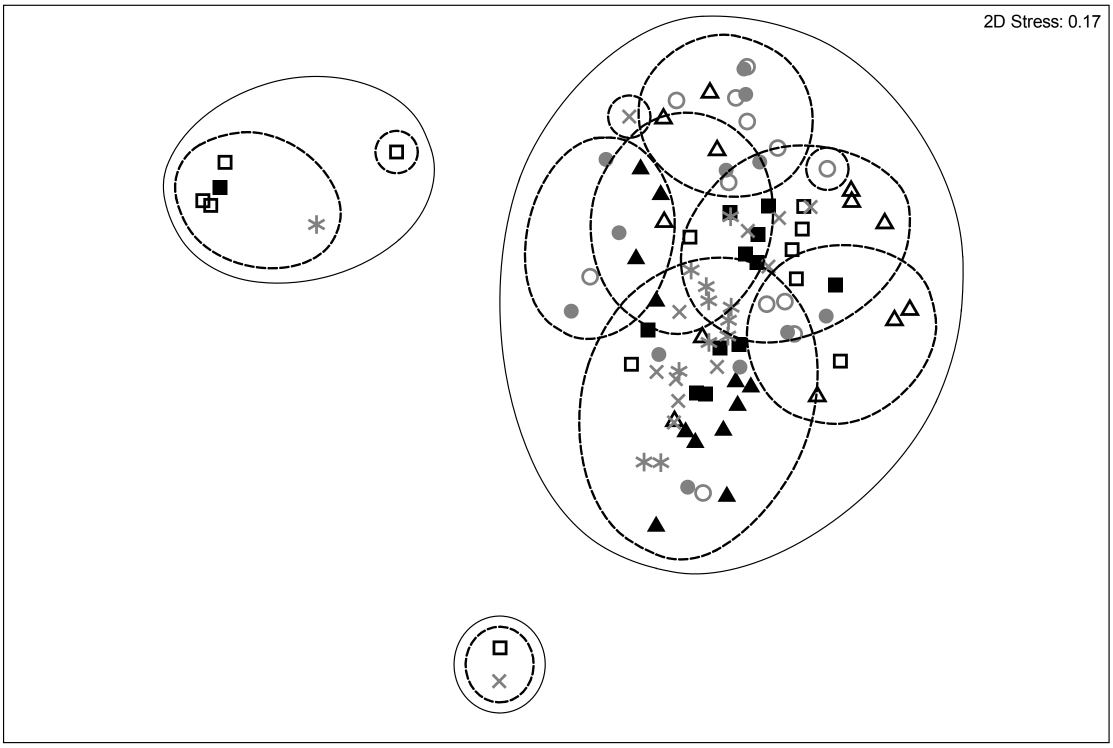


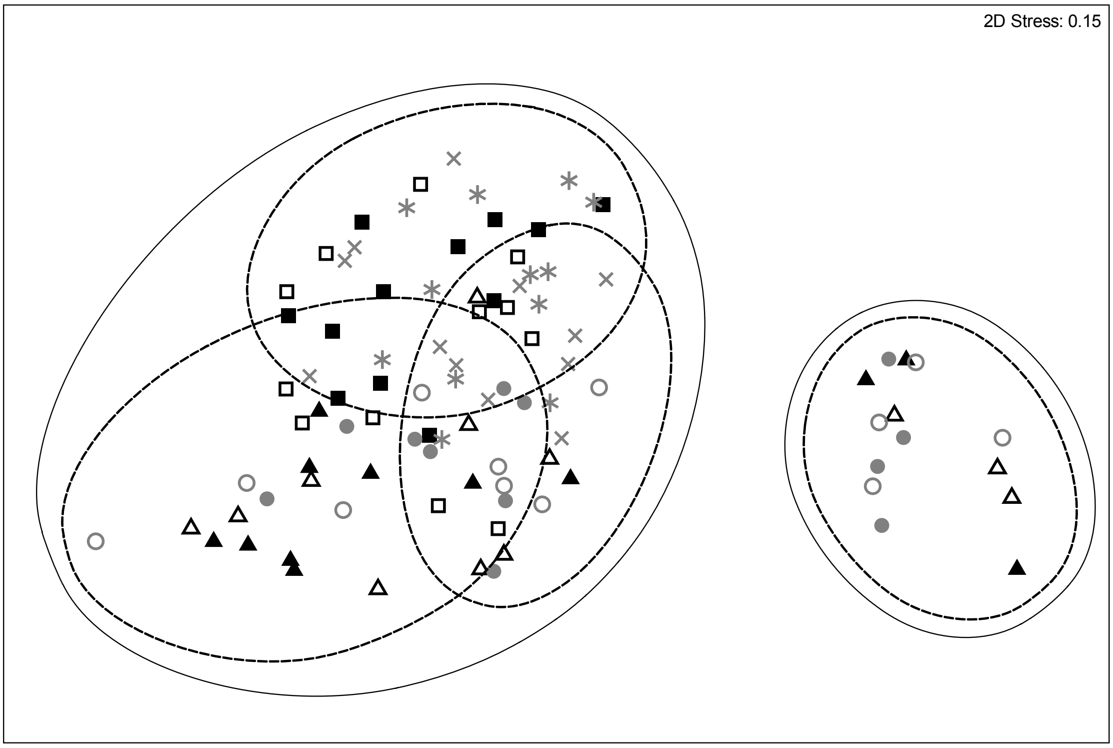
Figure 6.3: Total abundance of key taxa across each habitat type from 384 quadrat samples of dunging plots.

The NMDS ordinations for each habitat demonstrated that there was a high degree of similarity in plant species abundance between the factors (animal, treatment, worming regime) (Fig. 6.4). In grassland two outlier clusters were composed of control plots and the remaining central cluster consisted of overlapping treatments (Fig.6.4a). The heath ordination showed some separation of the worming factor shown in the right 40% similarity cluster which had no wormed sample plots within. Overlap was high for the rest of the samples (Fig.6.4b). Within mire some cattle natural control and treatment plots were distinct in a 60% similarity cluster (bottom right) while a large centre assemblage was highly similar (Fig.6.4c). In woodland, assemblages were the most distinct, with two main clusters at 40% similarity. The main left cluster (40% similarity) indicated differences in worming regime from the other main cluster and consisted of separate horse and cattle wormed plots. The other cluster (right) showed a high overlap for worming regimes and animal factors (Fig.6.4d). The ordinations indicated that dunging regime may answer the research question whether plant community response varies depending on dunging regime (research question i). The treatment factor was difficult to distinguish.

(a) GRASSLAND

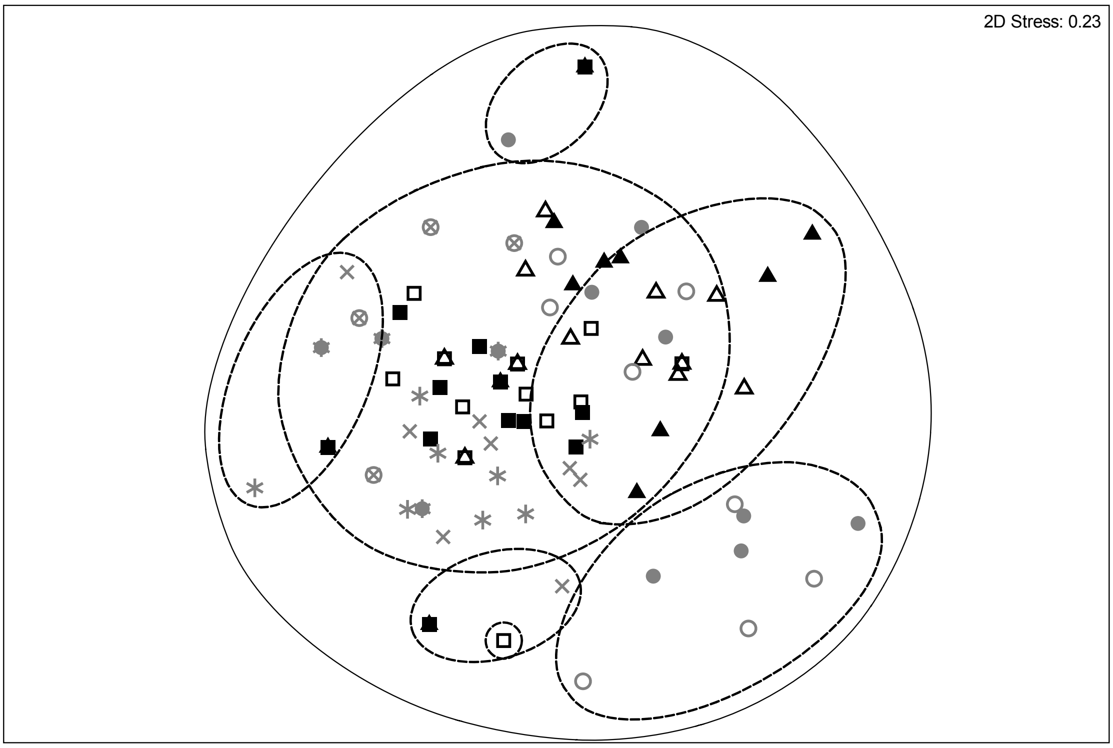


(b) HEATH



KEY: Δ Horse Natural Control, ▲ Horse Natural Treatment, □ Horse Wormed Control, ■ Horse Wormed Treatment, ○ Cattle Natural Control, ● Cattle Natural Treatment, × Cattle Wormed Control, ✱ Cattle Wormed Treatment

(c) MIRE



(d) WOODLAND

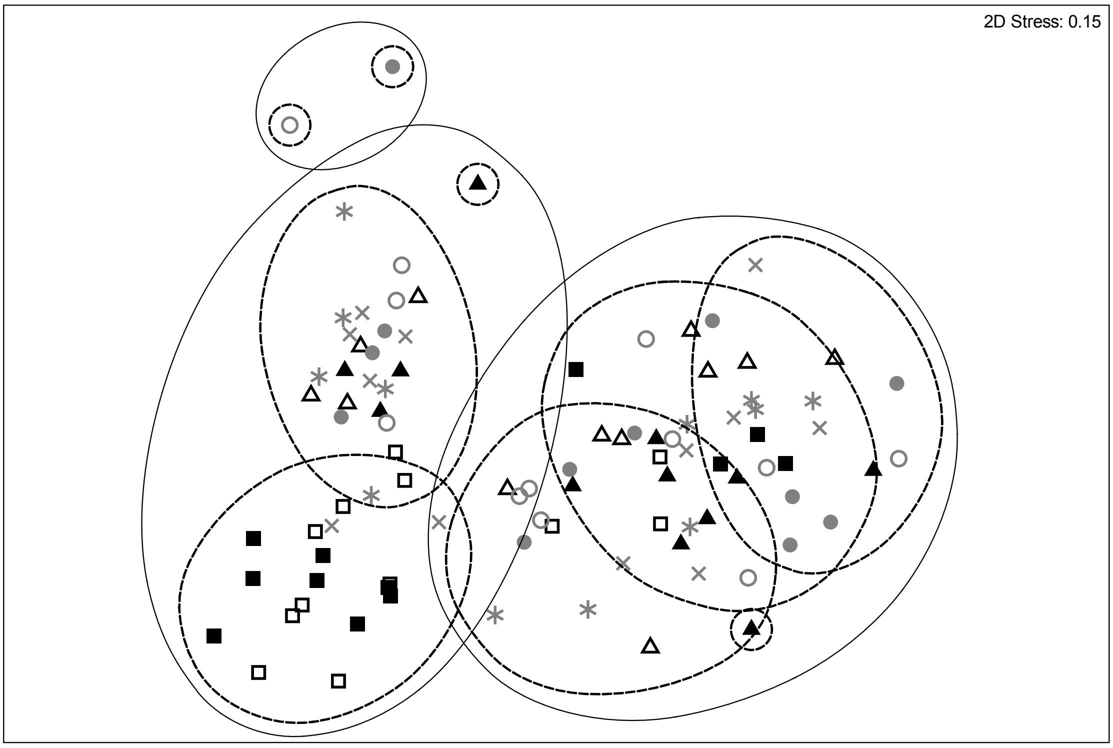


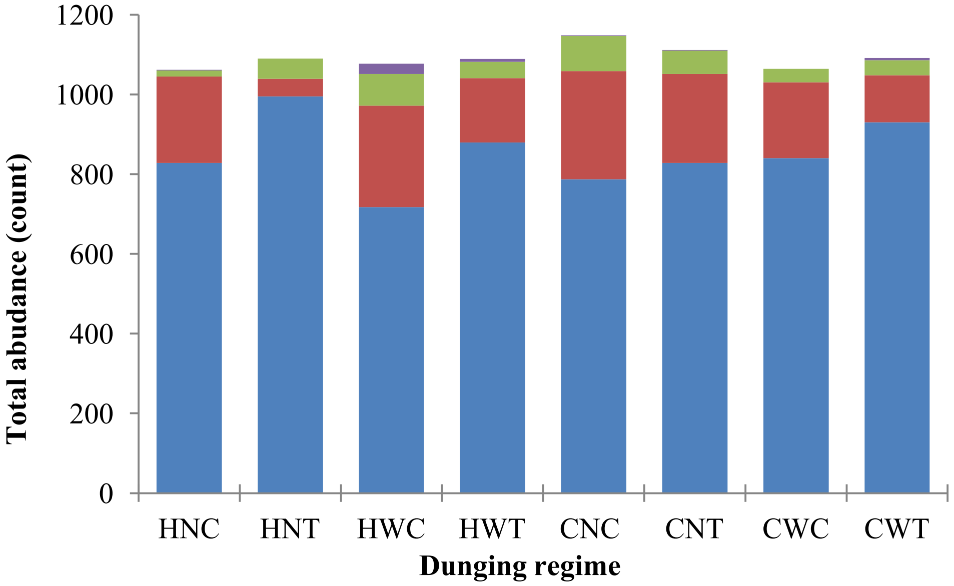
Figure 6.4(a-d) Non-metric multidimensional scaling ordinations for two dimensional space for each habitats 96 dunging quadrat samples with overlaid similarity clusters at 40% (solid line), 60% (dashed line). KEY: ∆ Horse Natural Control, ▲Horse Natural Treatment, □ Horse Wormed Control, ■ Horse Wormed Treatment, ○ Cattle Natural Control, ● Cattle Natural Treatment, × Cattle Wormed Control, ✱ Cattle Wormed Treatment.

6.3.2.2. Plant functional groups

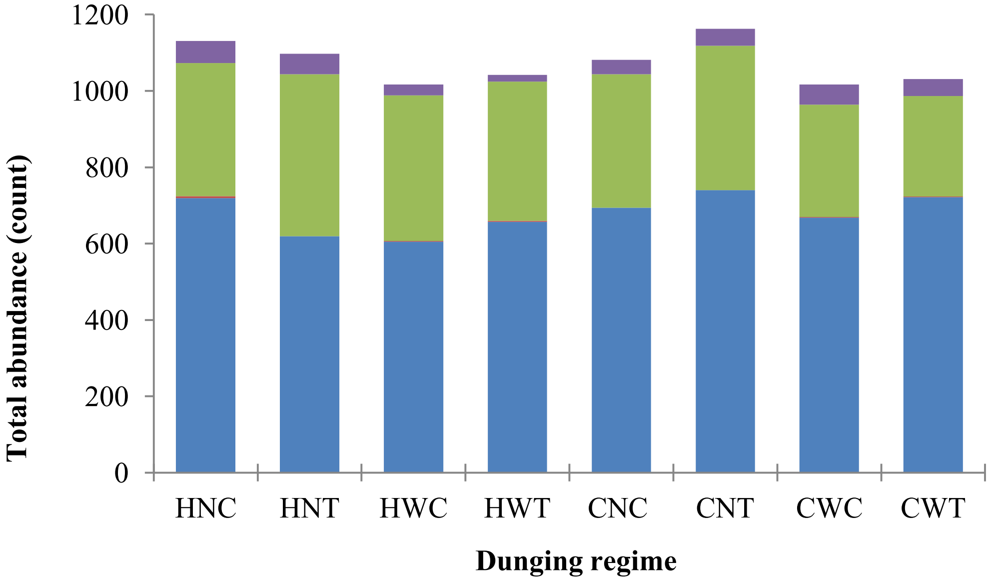
Examination of the relative abundances of graminoids and forbs (Fig. 6.5) indicated a difference between dunged and control plots in grassland which was supported by the highly significant increases for graminoids (*F*=19.350, *P*<0.001) and decrease for forbs (*F*=17.274, *P*<0.001) (Table 6.2). Graminoids were highly abundant in each habitat and forbs were only present in grassland, but a difference was displayed for worming regime in figure 6.5. The high abundance of ‘other’ plants in woodland and the difference between treatments was clear for horses, but not for cattle or the worming regime effect.

Analysis indicated that animal did have a different effect in mire, for other plants a reduction in dunged areas and an increase in woody plant abundance in woodlands. The three-way analysis of variance revealed a significant increase for worming regime due to animal in graminoids (*F*=17.834, *P*<0.001) and an interaction for forbs (*F*=9.757, *P*=0.002) in grassland. Woody plant abundance significantly responded to the interaction for treatment and worming regime due to animal (*F*=3.966, *P*=0.050) in grassland. Within heath there were significant decreases due to worming regime for all functional groups, most clearly seen in woody plants (Table 6.2)(Fig 6.5). In woodland, animal and worming effects showed separate differences for graminoids and for the interaction; this interaction was also observed in other plants (*F*=10.487, *P*=0.002) (Table 6.2) supported by the different abundances seen in Figure 6.5. The plant community when examined with plant functional groups was influenced by dunging regime, addressing research question (i) (*sub-section 6.1.4*).

(a) GRASSLAND

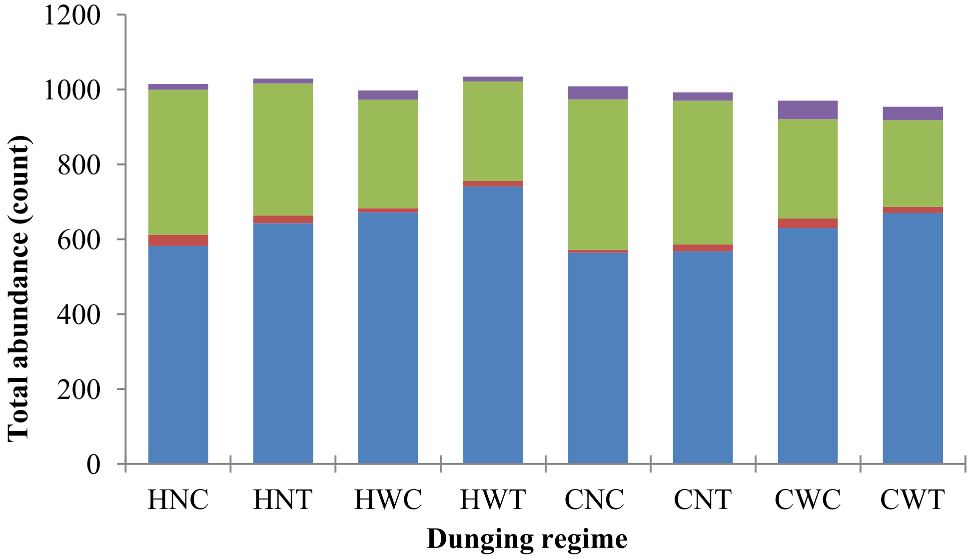


(b) HEATH



KEY: HNC (Horse Natural Control), HNT (Horse Natural Treatment), HWC (Horse Wormed Control), HWT (Horse Wormed Treatment), CNC (Cattle Natural Control), CNT (Cattle Natural Treatment), CWC (Cattle Wormed Control), CWT (Cattle Wormed Treatment).

(c) MIRE



(d) WOODLAND

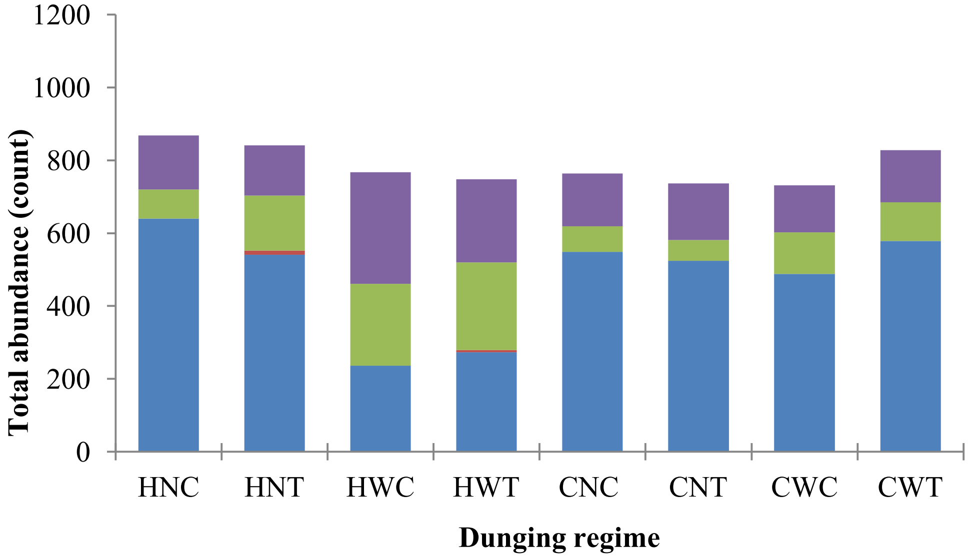


Figure 6.5: Relative abundance of plant functional group for dunging plots (a) grassland, (b) heath (c) mire and (d) woodland. Functional groups displayed from bottom to top: graminoids (BLUE), forbs (RED), woody plants (GREEN), other plants (PURPLE). HNC (Horse Natural Control), HNT (Horse Natural Treatment), HWC (Horse Wormed Control), HWT (Horse Wormed Treatment), CNC (Cattle Natural Control), CNT (Cattle Natural Treatment), CWC (Cattle Wormed Control), CWT (Cattle Wormed Treatment).

Table 6.2: *F*-statistics of three-way analysis of variance for plant functional group abundance in dunging plots

		GRASSLAND				HEATH				MIRE				WOODLAND			
						Plant functional group				Plant functional group				Plant functional group			
	d.f.	Graminoids	Forbs	Woody plants	Other plants	Graminoids	Forbs	Woody plants	Other plants	Graminoids	Forbs	Woody plants	Other plants	Graminoids	Forbs	Woody plants	Other plants
Between-subject																	
Animal	1	1.915	2.609	0.223	2.732	1.966	0.264	3.756	0.574	0.922	0.027	0.009	8.970**	12.717**	2.000	9.624**	2.302
Worming regime	1	0.006	0.034	0.045	3.758	12.304**	15.196***	6.224*	20.487***	13.710***	0.367	15.211***	1.679	18.465***	0.000	13.898***	3.665
Treatment	1	19.350***	17.274***	0.380	1.263	0.001	0.002	0.001	0.116	2.279	0.001	1.310	1.671	0.095	2.000	0.073	0.020
Animal x Worming regime	1	17.834***	9.757**	4.858*	3.304	0.628	0.337	0.290	0.302	0.012	1.783	0.389	0.574	17.642***	0.000	0.419	10.487**
Animal x treatment	1	2.921	2.693	0.288	3.665	0.219	0.006	0.258	0.015	0.067	0.158	0.036	0.064	1.100	2.000	2.334	0.138
Worming regime x Treatment	1	0.064	0.406	2.527	0.374	0.562	0.002	0.723	0.115	0.107	0.001	0.013	0.000	0.120	0.000	0.169	0.113
Animal x Worming regime x Treatment	1	0.208	2.679	3.966*	1.987	0.249	0.012	0.207	0.001	0.215	2.010	0.057	0.041	0.329	0.000	1.324	0.286
Error	88	74.670	96.707	52.478	13.163	118.701	167.173	120.277	82.966	62.464	35.664	66.178	42.810	205.966	10.551	117.727	205.108
Total	96																

*Significant at *P<0.05* ** Significant at *P<0.01* ***Significant at *P<0.001*

6.3.2.3. Key species

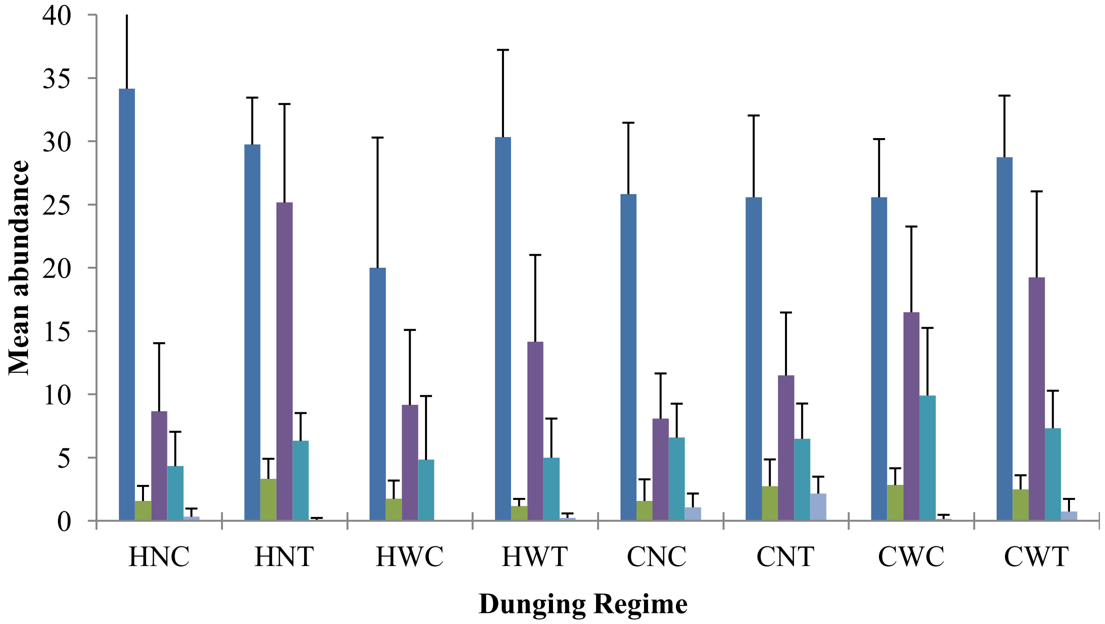
Findings for the key species backed those of the plant functional group (Figs. 6.5 and 6.6). Within grassland, *Agrostis* displayed a higher mean abundance in dunged plots for all factors (animal and worming) except in the horse non-wormed "natural" plots, although variance in control plots was large. There was only a significant interaction between animal and worming regime (*F*= 4.744, *P*=0.032) and worming and treatment (*F*= 4.274, *P*=0.042) (Table 6.3a) for this plant. Abundant *Molinia*, closely followed the effects seen in the graminoids and showed a significant increase in abundance for dunging (*F*= 10.181, *P*=0.002) and for animal and worming regime (*F*= 8.735, *P*=0.099). Effects of animal were only evident for *Carex* (*F*= 4.344, *P*=0.040) and *Calluna* (*F*= 9.107, *P*=0.003) and differences in abundances were significant for animal and worming factors in *Calluna* (*F*= 4.072, *P*=0.0470) (Table 6.3a).

The different compositions within heath meant a differing response was observed (Fig. 6.3). For *Calluna*, the differences between factors were not significant and variances were high, although a difference between animals was evident (e.g. low mean abundances for cattle) (Fig. 6.6b) but not significant (*F*= 2.832, *P*=0.096) (Table 6.3b). For *Carex* and *Molinia,* differences were observed within the probability level of 5% (*Carex: F*= 4.010, *P*=0.048), with higher abundances for cattle dunging for *Molinia* (*F*= 8.847, *P*=0.004). For *Molinia* there was also a significant interaction for all three factors (animal x worming regime x treatment) (*F*= 4.427, *P*=0.038). The worming plots had lower means in all key species except *Agrostis* where there was a significant difference (*F*= 35.220, *P*<0.001); supported by a difference for worming in the ordination plot (Table 6.4b).

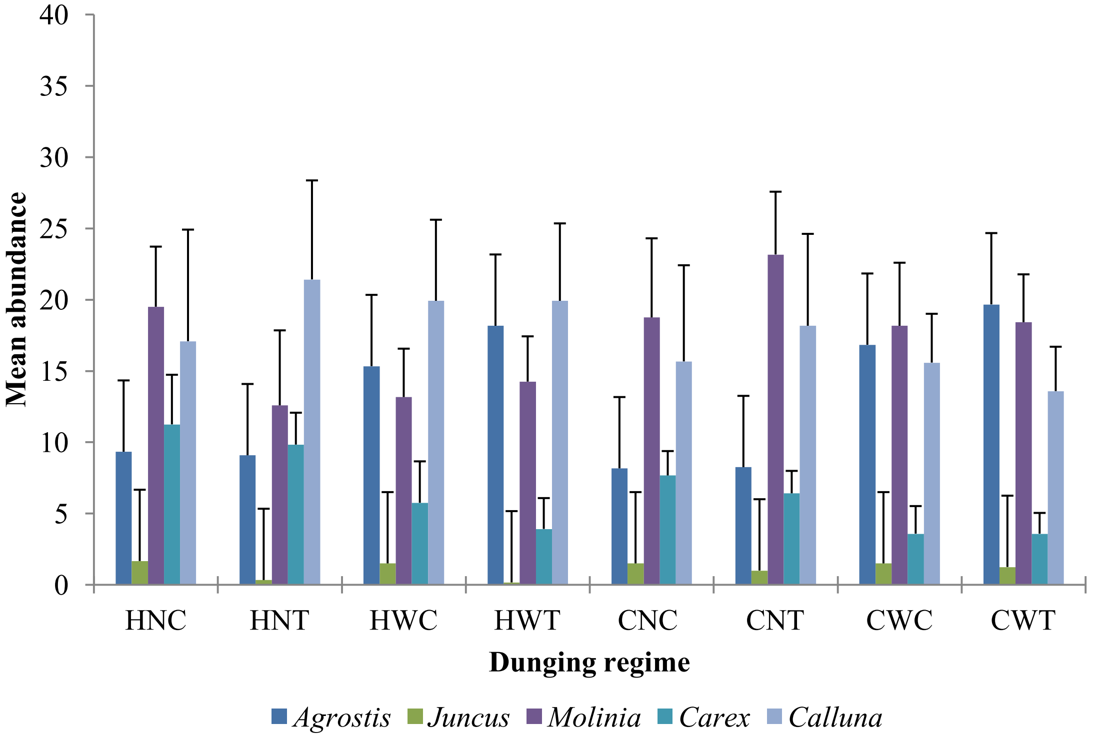
Molinia was an abundant species in mire (Fig. 6.3) and there were observed differences between horses and cattle (*F*= 10.002, *P*=0.002), as well as for *Calluna* (*F*= 4.941, *P*=0.029) which was also significantly different for worming regime (*F*= 10.147, *P*=0.002) (Table 6.3c).

Differences between the mean abundances for the effects of worming regime was apparent in *Agrostis* (*F*= 6.307, *P*=0.014) and *Carex* (*F*= 4.231, *P*=0.043) in woodland. *Juncus* was significantly different between horses and cattle (*F*= 4.008, *P*=0.048) and

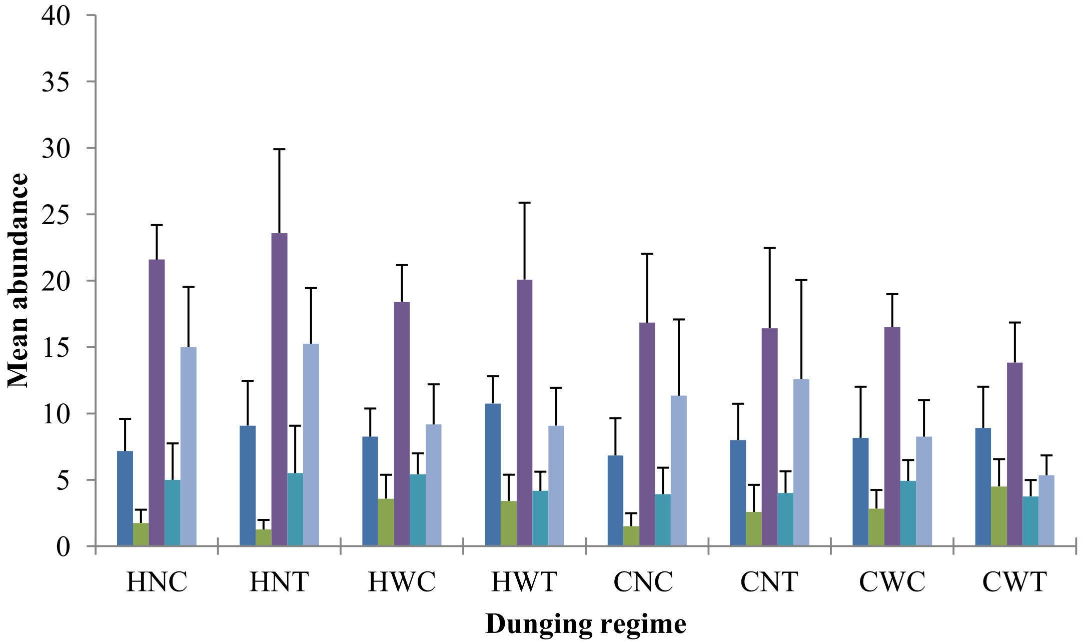
(a) GRASSLAND



b) HEATH



c) MIRE



d) WOODLAND

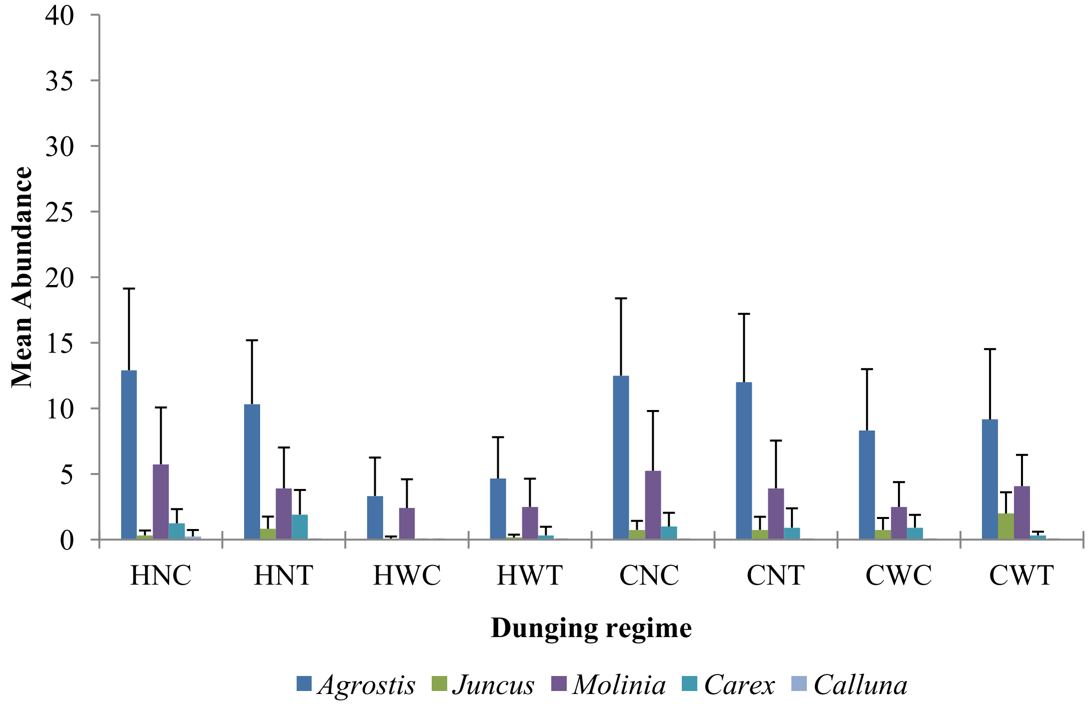


Figure 6.6a-d: Mean abundance of key species for animal, worming and treatment effects in 384 dunging quadrat samples with 95% confidence intervals. (a) Grassland, (b) Heath, (c) Mire, (d) Woodland. HNC (Horse Natural Control), HNT (Horse Natural Treatment), HWC (Horse Wormed Control), HWT (Horse Wormed Treatment), CNC (Cattle Natural Control), CNT (Cattle Natural Treatment), CWC (Cattle Wormed Control), CWT (Cattle Wormed Treatment).

cattle had higher mean abundances; a difference in treatment was observed in Figure 6.6d, but this was not significant.

As the control plots for wormed and natural treatments were treated equally in terms of no faecal application, outlined in the Chapter 2 General Methods (*section 6.2.3*), a *t*-test examined if there were any significant differences. The findings indicated that there were minimal significant differences ($P \leq 0.05$) for *Agrostis*, *Molinia* and *Carex* in grassland and woodland horse plots and heath horse and cattle plots (Appendix 15), although *t*-values were not large.

Table 6.3(a-d): *F*-statistics from three way analysis of variance for key taxa abundance for dunging plots. *Calluna* was absent from woodland abundance data (denoted by -).

(a) Grassland

		Key taxa				
Between-subject effects	*d.f.*	*Agrostis*	*Juncus*	*Molinia*	*Carex*	*Calluna*
Animal	1	0.000	0.712	0.135	4.344*	9.107**
Worming regime	1	3.047	0.174	0.050	0.197	4.840*
Treatment	1	1.776	1.704	10.181**	0.090	2.254
Animal x Worming	1	4.774*	3.833	8.735**	2.016	4.072*
Animal x Treatment	1	0.655	0.079	2.785	0.960	1.146
Worming x Treatment	1	4.274*	1.383	0.675	0.428	0.012
Animal x Worming x Treatment	1	1.997	0.068	0.774	0.005	0.882

(b) Heath

		Key taxa				
Between-subject effects	*d.f.*	*Agrostis*	*Juncus*	*Molinia*	*Carex*	*Calluna*
Animal	1	0.146	3.832	8.847**	4.010*	2.832
Worming regime	1	35.220***	0.229	1.320	34.508***	0.000
Treatment	1	0.949	5.160*	0.027	0.971	0.359
Animal x Worming	1	0.744	0.063	0.006	1.260	0.384
Animal x Treatment	1	0.028	2.500	3.502	0.491	0.161
Worming x Treatment	1	0.571	0.075	0.530	0.018	1.403
Animal x Worming x Treatment	1	0.038	0.361	4.427*	0.733	0.005

*Significant at *P*<0.05; **Significant at *P*<0.01; ***Significant at *P*<0.001

(c)Mire

		Key taxa				
	d.f.	*Agrostis*	*Juncus*	*Molinia*	*Carex*	*Calluna*
Between-subject effects						
Animal	1	0.937	0.292	10.002**	0.172	4.941*
Worming regime	1	2.105	8.643**	1.049	0.644	10.147**
Treatment	1	2.328	0.049	0.063	0.179	0.183
Animal x Worming	1	0.152	0.016	0.647	0.006	0.125
Animal x Treatment	1	0.004	1.700	0.852	0.012	0.362
Worming x Treatment	1	0.049	0.015	0.114	0.735	0.714
Animal x Worming x Treatment	1	0.207	0.057	0.109	0.000	0.439

(d)Woodland

		Key taxa				
	d.f.	*Agrostis*	*Juncus*	*Molinia*	*Carex*	*Calluna*
Between-subject effects						
Animal	1	1.407	4.008*	0.134	0.050	-
Worming regime	1	6.307*	0.018	0.817	4.231*	-
Treatment	1	0.003	1.096	0.042	0.040	-
Animal x Worming	1	0.883	2.144	0.646	3.424	-
Animal x Treatment	1	0.001	0.051	0.262	0.835	-
Worming x Treatment	1	0.253	0.603	1.127	0.018	-
Animal x Worming x Treatment	1	0.102	1.099	0.081	0.026	-

*Significant at $P<0.05$; **Significant at $P<0.01$; ***Significant at $P<0.001$

6.3.3. Sward height

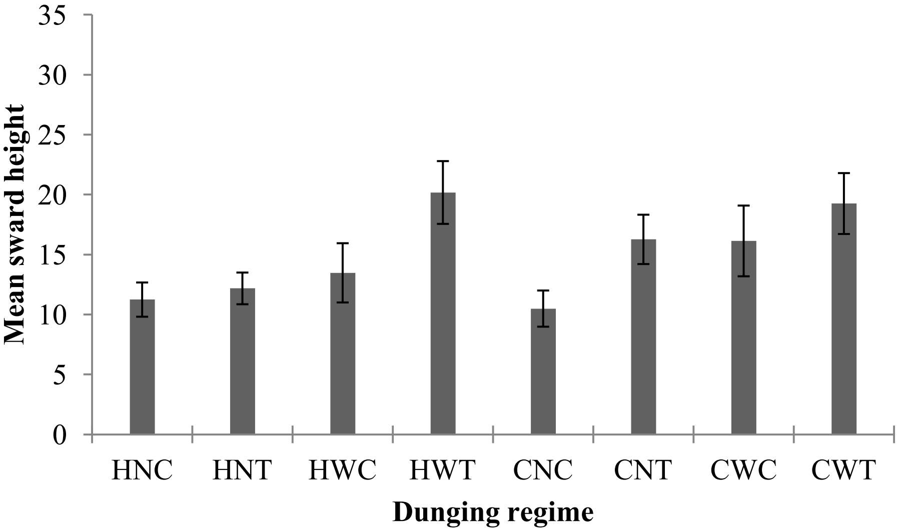
Sward height only responded significantly differently to the main effect of animal in woodland (*F*=7.077, *P*=0.008), where the heights from cattle plots were slightly higher than horses (Fig. 6.7). The height was significantly different due to worming in the grassland (*F*=23.107, *P*<0.001), heath (*F*=22.084, *P*<0.001) and mire (*F*=25.456, *P*=0.001) (Table 6.4), although the response was varied with moderate variances (Fig 6.7). In heath, sward height responded differently to worming regime based on animal (*F*=3.849, *P*=0.050) and also for worming regime and treatment (*F*=5.151, *P*=0.024). A significant interaction for all three factors (Animal x Worming regime x Treatment) was observed in grassland (*F*=10.436, *P*=0.001), populated by successional species such as *Agrostis* and *Molinia*, supporting the findings of plant composition (Figs. 6.5 and 6.6), which contributed to satisfying research question (ii).

Table 6.4: *F*-statistics from three-way analysis of variance for sward height within each habitat assemblage for dunging plots

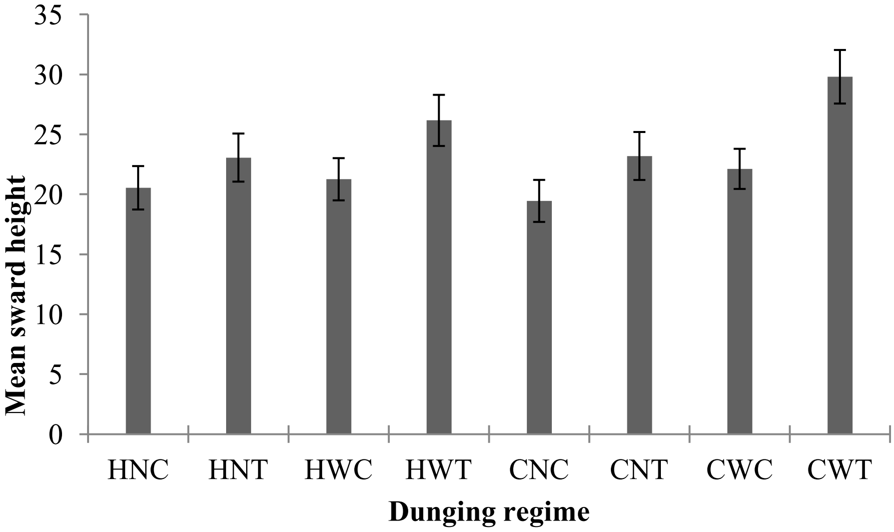
		Habitat type			
	d.f.	Grassland	Heath	Mire	Woodland
Between-subject effects					
Animal	1	1.161	1.619	0.011	7.077**
Worming	1	23.107***	22.084***	25.456***	3.066
Treatment	1	48.204***	45.817***	69.058***	1.054
Animal x Worming	1	0.009	3.849*	2.266	0.740
Animal x Treatment	1	0.086	2.067	1.962	0.555
Worming x Treatment	1	0.602	5.151*	1.202	0.107
Animal x Worming x Treatment	1	10.436**	0.308	0.012	0.735

*Significant at *P*<0.05; **Significant at *P*<0.01; ***Significant at *P*<0.001

(a) GRASSLAND


35
30
25
20
15
10
5
0
Mean sward height
HNC
HNT
HWC
HWT
CNC
CNT
CWC
CWT
Dunging regime

(b) HEATH


35
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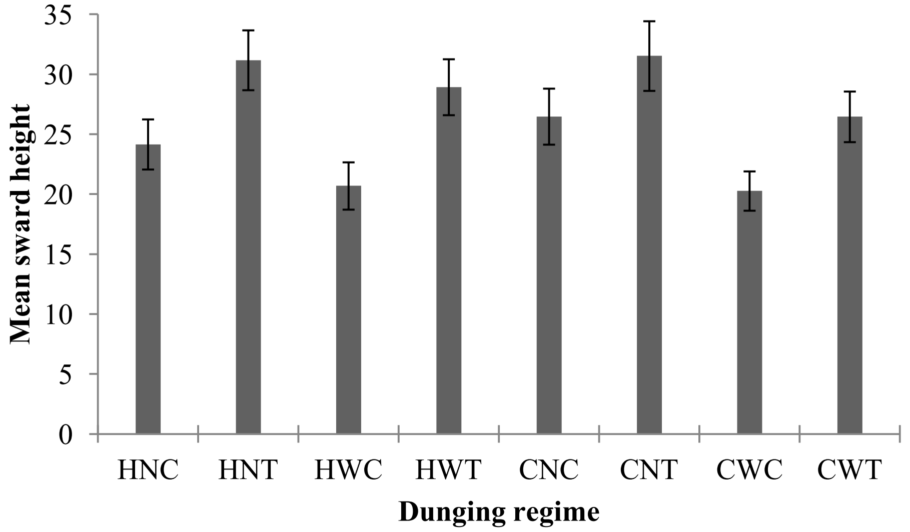
Mean sward height
HNC
HNT
HWC
HWT
CNC
CNT
CWC
CWT
Dunging regime

(c) MIRE



(d) WOODLAND

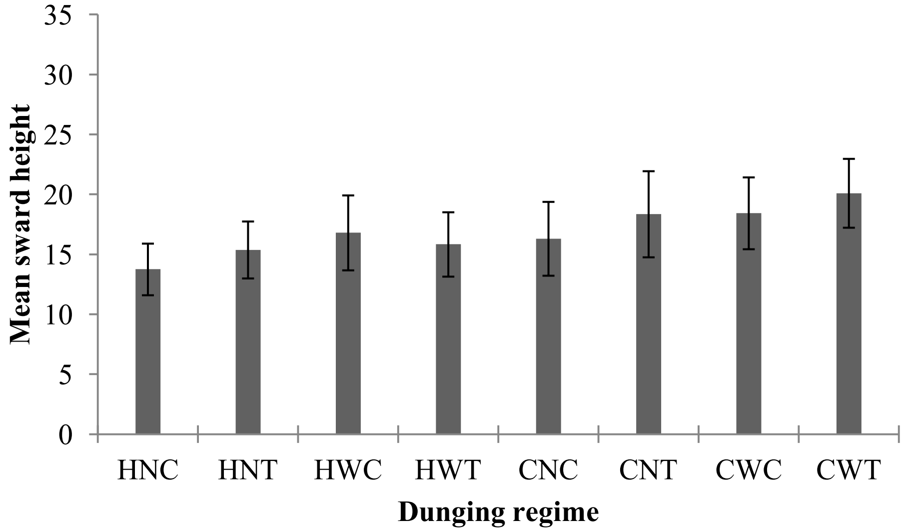
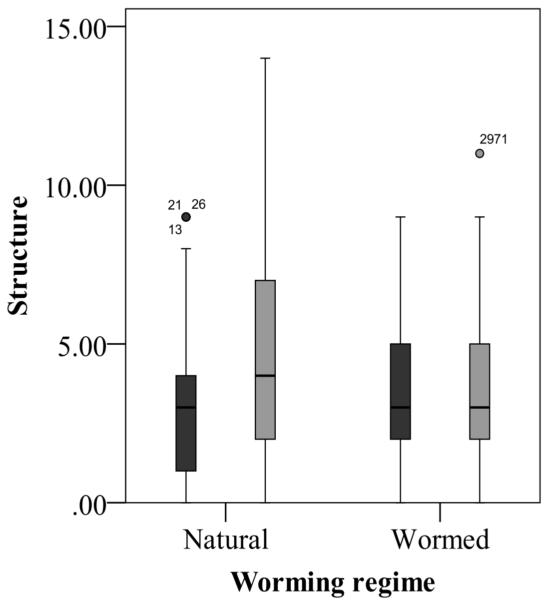


Figure 6.7a-d: Mean sward heights for dung treatment plots for both animals across the four habitat assemblages: (a) Grassland, (b) Heath, (c) Mire, (d) Woodland. HNC (Horse Natural Control), HNT (Horse Natural Treatment), HWC (Horse Wormed Control), HWT (Horse Wormed Treatment), CNC (Cattle Natural Control), CNT (Cattle Natural Treatment), CWC (Cattle Wormed Control), CWT (Cattle Wormed Treatment). Error bars represent 95% confidence intervals.

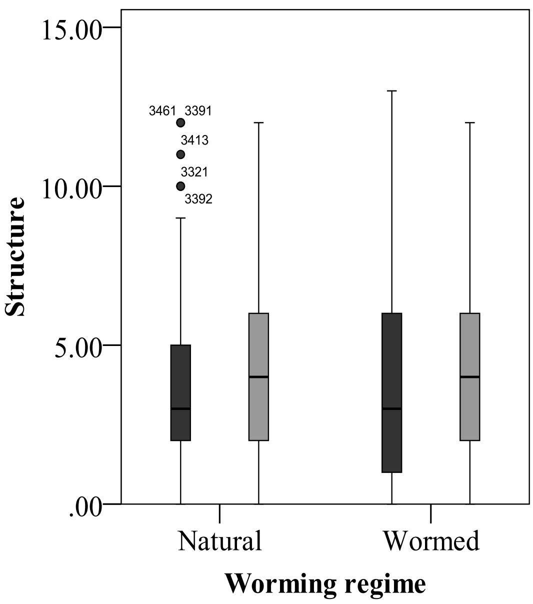
6.3.4. Structural heterogeneity

Examination of the medians of the structural intercepts for each animal within each habitat (Fig. 6.8) demonstrated significant differences in the distributions between worming treatments in all habitats except grassland (Table 6.5). Significant differences in treatment effects were clear in all habitats apart from woodland. Animal effects were not very apparent in the box-plots, although the statistic was evidently large in mire (F=127.039, P<0.001) and worming regime had highly significant effects on mire and woodland (Mire: F=696.132, P<0.001; Woodland: F=455.177, P<0.001) (Table 6.5). Variances were high in all factors due to the large sample size (n=9600) and there were outliers in all, particularly in mire and woodland.

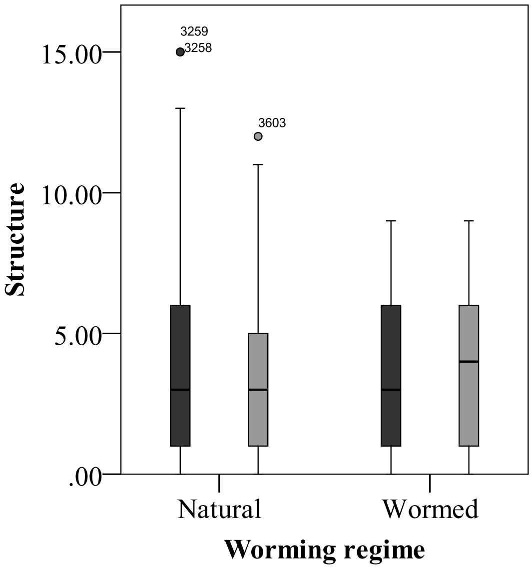
(A) GRASSLAND HORSE



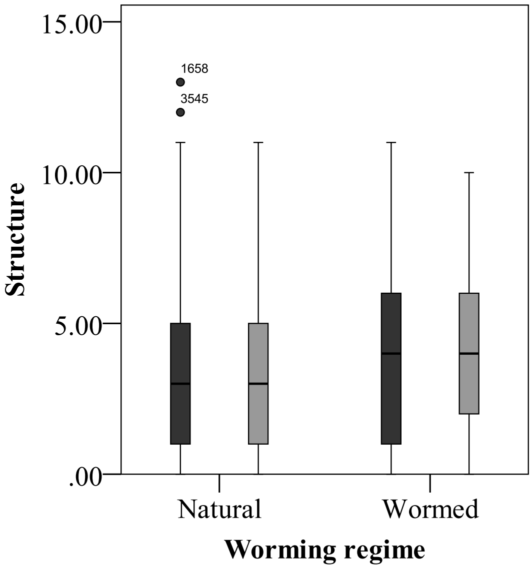
(B) GRASSLAND CATTLE



(C) HEATH HORSE



(D) HEATH CATTLE



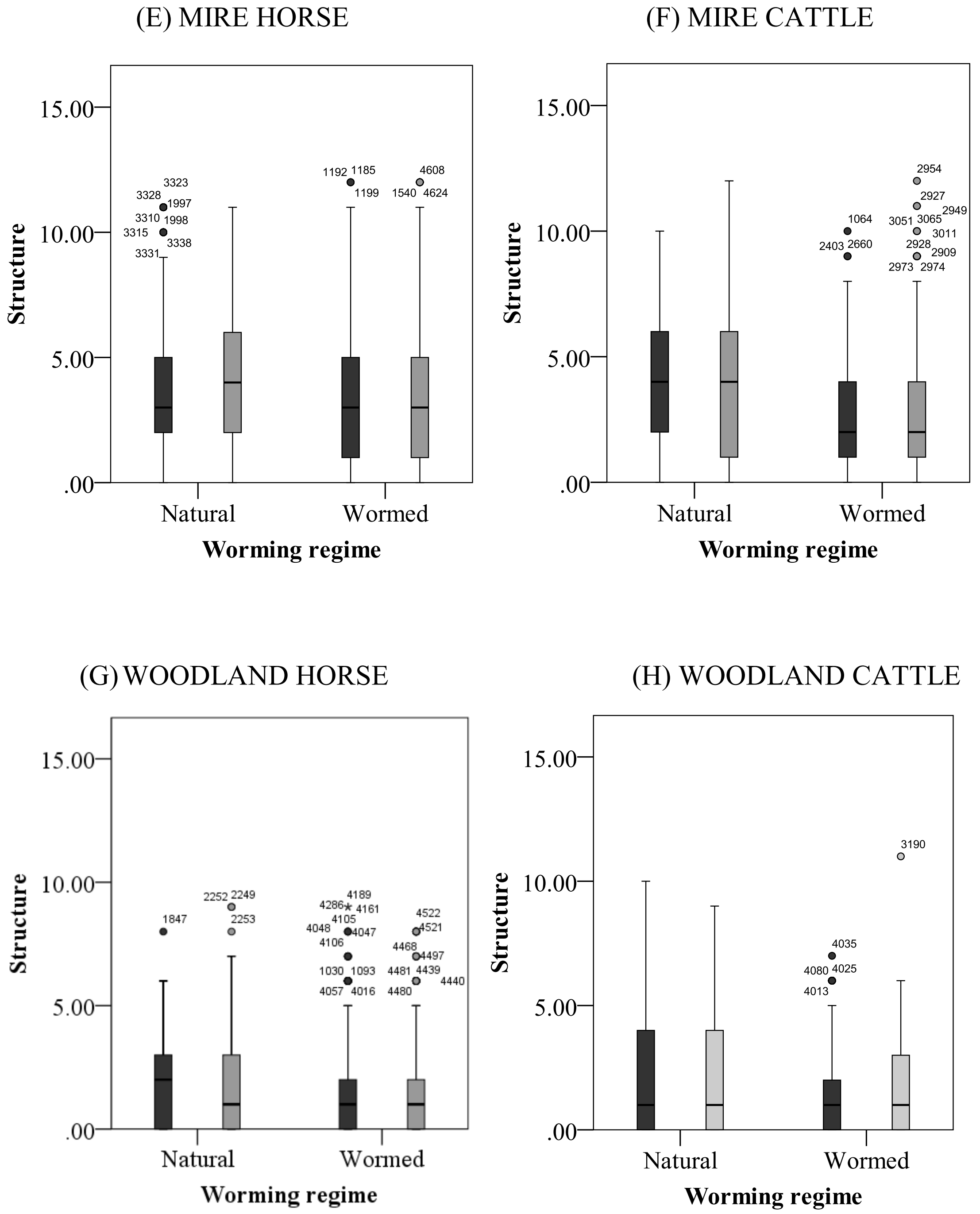


Figure 6.8a-h: Box-plots of structural intercepts for dunging plots for each animal within each habitat. Control: dark grey, Treatment: light grey.

The interaction between animal and worming was highly significantly different for mire (*F*=154.844, *P*<0.001), as were the individual effects (Table 6.5). Worming and treatment interactions were highly significant in grassland (*F*=92.730, *P*<0.001). The interaction between all three factors (animal x worming regime x treatment) was displayed in grassland (*F*=23.837, *P*<0.001), heath (*F*=4.119, *P*=0.042) and woodland (*F*=15.281, *P*<0.001). The significant statistics may be an indication of large sample size (n=9600), but indicating small differences in the plant structure. Interactions for treatment and worming regime based upon animal were also exhibited (Table 6.5).

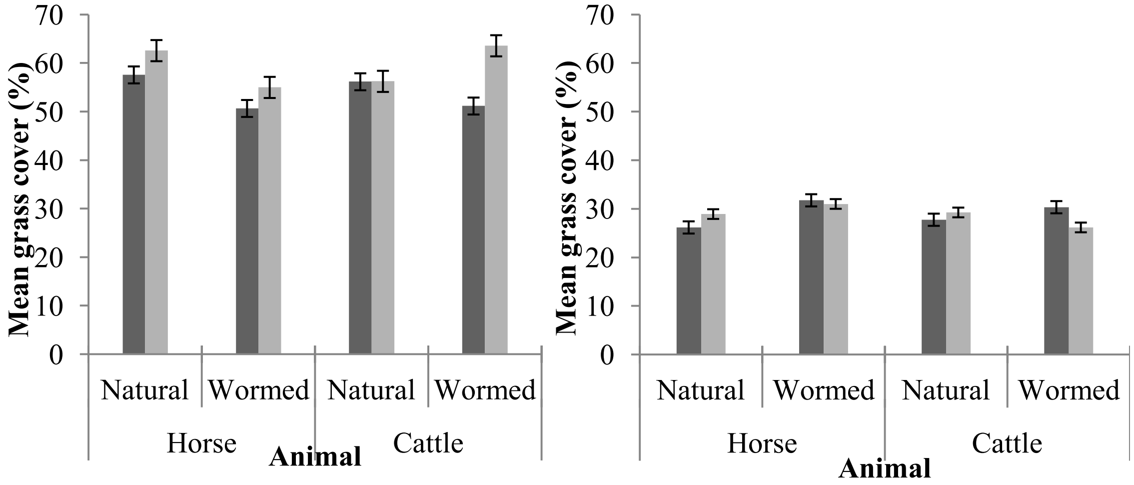
Table 6.5: Wald chi-square statistics for tests of structural difference between the dunging main effects using a Generalized Linear Model (n=9600).

	d.f.	*Grassland*	*Heath*	*Mire*	*Woodland*
Wald Chi-square statistics					
Animal	1	23.808***	2.444	127.039***	77.228***
Worming	1	0.193	38.511***	696.132***	455.177***
Treatment	1	162.630***	30.380***	16.690***	0.329
Animal x Worming	1	0.195	4.338*	154.844***	48.773***
Animal x Treatment	1	13.374***	3.662	7.059**	36.927***
Worming x Treatment	1	92.730***	6.840**	3.038	1.213
Animal x Worming x Treatment	1	23.837***	4.119*	0.011	15.281***

*Significant at *P<0.05;* **Significant at *P<0.01;* ***Significant at *P<0.001*

6.3.5. Spatial heterogeneity

Marked differences between animals were not clear in any of the habitats, except for woodland (Fig. 6.9). There were minimal differences in grass cover between worming regimes for grassland, heath and mire, but were distinct as the variances were small. Woodland displayed the largest differences between natural and wormed regimes, particularly for horses which showed an opposite effect to cattle in the same habitat (Fig. 6.9d), but there were no significant differences between treatments. Grass cover was higher in non-dunged compared to dunged areas within grassland, but the other habitats showed variable responses.



(a) Grassland

(b) Heath

(c) Mire

(d) Woodland

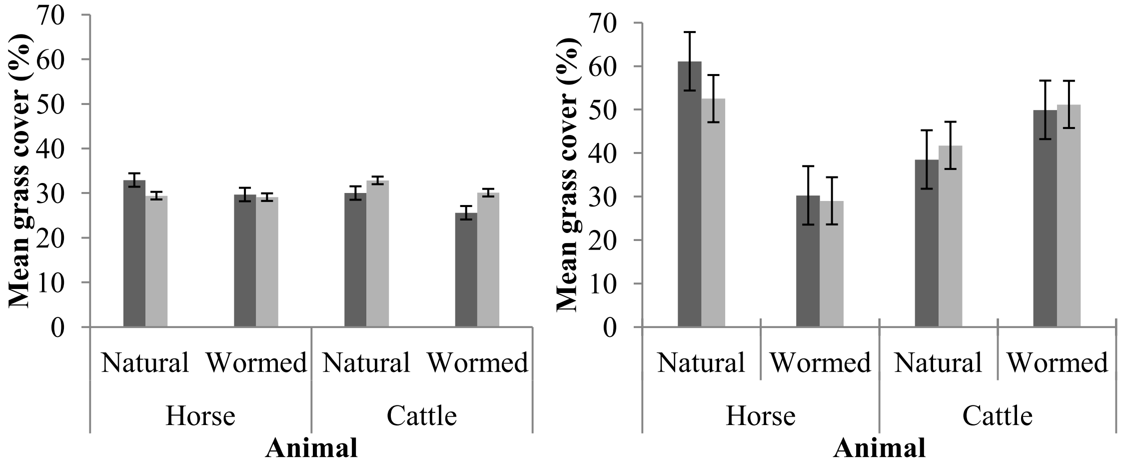


Figure 6.9a-d: Mean percentage grass cover for all plots of animal, worming regime and dunging treatment factors, with standard errors. (n=48). Dark grey: Control (non-dunged) regime; Light grey: Treatment (dunged regime).

The only significant difference exhibited for the interaction was for animal and worming in woodland (*F*=15.415, *P*<0.001) (Table 6.6), which supported the large differences in cover exhibited in the woodlands (Fig. 6.9d). The grass cover differed between worming regimes for horses and cattle on grassland but the interaction was not significant (animal x worming regime: *F*=1.720, *P*=0.193) (Fig 6.9). The interaction for all factors was also not significant in any habitat, although grassland had the highest *F*-statistic (animal x worming regime x treatment: *F*=1.056, *P*=0.307).

Table 6.6: *F*-statistics from three-way analysis of variance of grass cover for each habitat for dunging plots (n= 48).

Between-subject effects	*d.f.*	*Grassland*	*Heath*	*Mire*	*Woodland*
Animal	1	0.019	0.238	0.080	0.376
Worming regime		0.719	0.566	1.953	2.314
Treatment	1	2.831	0.006	0.169	0.078
Animal x Worming		1.720	1.062	0.296	15.415***
Animal x Treatment	1	0.062	0.499	2.581	0.584
Worming x Treatment	1	0.863	1.211	0.374	0.011
Animal x Worming x Treatment	1	1.056	0.079	0.038	0.207

*Significant at *P<0.05;* **Significant at *P<0.01;* ***Significant at *P<0.001*

The soil chemical properties, analysed with multiple regression across all habitats, revealed that there was a causal relationship for phosphorus (B=3.811, *t* =2.758, *P*=0.007) and pH (B=8.034, *t* =2.176, *P*=0.032) with grass cover (intercept= -22.857, *t* = -1.267, *P*=0.208). The B coefficient, the slope of the regression line, indicated a significant positive relationship for both phosphorus and pH with a *t*-value testing the null hypothesis that the slope is equal to zero. For both covariates the effect was significant (*P*<0.05). The intercept *t*-value indicated that it was equal to zero (*P*>0.05). Nearly 26% of the variation in grass cover was significantly explained (*R squared* =0.255, *F*=7.781, *P*<0.001) by the model and the variation in these soil properties.

The analysis of covariance indicated there was a significant interaction between worming regime and treatment in grassland (*F*=4.877*, P*=0.044) (Table 6.7). The covariates were not significant (*P*>0.05). In heath worming regime showed significant effects (*F*=8.620, *P*=0.011) and woodland displayed that there was a highly significant interaction between animal and worming regime (*F*=32.659, *P*<0.001), covariates were not significant. A significant effect for pH as a covariate (*F*=5.697, *P*=0.032) was exhibited in mire. The factor of animal was also significantly different in this habitat (*F*=10.851, *P*=0.005) (Table 6.7). These findings addressed research question (iv) (*sub-section 6.1.4*) that asked if soil chemical properties were causal factors for spatial heterogeneity. It also addressed the question whether there was an impact of soil chemical properties (i.e. pH) from dunging regime on spatial heterogeneity, for grass cover.

Table 6.7: *F*-statistics for analysis of covariance of grass cover for main dunging regime effects with covariates (n=24).

	d.f.	Grassland	Heath	Mire	Woodland
Between-subject effects					
pH	1	0.768	3.977	5.697*	3.518
P	1	0.086	1.239	0.025	3.105
Animal	1	0.000	0.606	10.851**	0.548
Worming regime		0.390	8.620*	0.059	0.027
Treatment	1	0.348	1.271	0.893	0.145
Animal x Worming		1.675	0.005	0.946	32.659***
Animal x Treatment	1	1.416	1.211	0.058	0.064
Worming x Treatment	1	4.877*	0.374	1.258	0.004
Animal x Worming x Treatment	1	3.995	0.825	2.328	0.071

*Significant at *P<0.05,* **Significant at *P<0.01,* ***Significant at *P<0.001.*

6.4. Discussion

The changes to the composition of vegetation and its physical attributes were highly influenced by dunging and were observed over the short experimental period. The dunging regimes were representative of low-level grazing management on lowland heath, which experimentally had not been achieved previously (Newton et al., 2009). Worming regime, specifically, had not been examined in lowland heath in terms of the effects on vegetation through nutrient availability and delayed faecal degradation (Madsen et al., 1990, Iglesias et al., 2006). The outcomes meant that the general aims of the chapter were achieved and informed grazing management because of an improved understanding of dunging impacts.

6.4.1. Vegetation change to nutrient availability

The effect of increasing nutrient availability in this study resulted in architectural changes to sward height and structure, related to the plant composition, as reported in other dunging studies (Williams and Haynes, 1995, Kohler, 2004, Gillet et al., 2010). Nutrient addition has been found to increase litter production and decomposition related to the increased nutrient mobilisation through microbial activity (Barker et al., 2004), especially in relation to water availability (Jensen et al., 2003). The repeated application of dung in this study increased influential nutrients (e.g. nitrogen and phosphorus) eventually altering the competitive balance between plants (Crawley, 1983, Kohler et al., 2004) through an increase in graminoid abundance on grassland, particularly for dominant plant species (e.g. *Molinia*) (Table 6.2 and 6.3) (Dai, 2000, Gillet et al., 2010).

The increase in grasses and decrease in forbs supported other heathland-specific studies (Bakker et al., 1983) owing to enhanced fertility in grassland (Fig. 6.5)(Table 6.2), despite the differences in grazing regime (i.e. sheep dunging and combined grazing) (Bakker et al., 1983). The trends are comparable to those observed in mountain pasture (Kohler et al., 2004). Such compositional changes, owing to improved fertility (Hartley and Mitchell, 2005), were supported by an increased structural complexity in dunged plots (Fig. 6.8). This structure was likely to be positively related to sward height (Fig. 6.7) and increased vegetation density (Schwab et al., 2002, Hulme et al., 2003). It was not possible to perform a correlation between these parameters as the sampling points were not comparable. Nutrient availability was governing but sward heterogeneity also determined the vegetation response.

6.4.2. Spatially-variable response

Vegetation responds to dunging in a spatially-variable way at a patch-level (Hartley and Mitchell, 2005). The complex and finer-scale interactions between plant, soil and dung showed a differential response owing to the life history traits of the plants (Williams and Haynes, 1995, Jørgensen and Jensen, 1997), i.e. between graminaceous plants and woodier plants. Graminaceous plants that could readily utilise the nitrogen available rapidly grew in the sward (Gillet et al., 2010) while herbaceous plants like *Calluna* showed minimal effects (Table 6.3) (Bokdam, 2001). Propagule transport or seed dispersal by dunging may also have been a factor for the heterogeneous plant response (Cosyns et al., 2005, Cosyns and Hoffmann, 2005), although this mechanism was not tested.

A structurally heterogeneous response was observed owing to the effects of canopy height and density (Table 6.4 and 6.5) (Schwab et al., 2002, Hulme et al., 2003), but differences in sward spatial heterogeneity (e.g. grass cover) between treatments, were limited (Table 6.6 and 6.7). Grass cover has been shown to be highly influenced by nutrient addition on upland heath (Hartley and Mitchell, 2005), but plant response in the documented study responded to dunging combined with grazing. The homogenous application of dung may have also reduced any heterogeneous response, although the differences between upland and lowland heath or between habitats may have had some effect.

6.4.3. Lowland heath dynamics

The sensitivity of lowland heath vegetation to modification by enrichment is critical because of the impoverished and acidic soil (Gimingham, 1972, Bullock and Pakeman, 1997, Barker et al., 2004) (see soil chemical compositions, appendices 4 and 12). Indeed, the typical dwarf-shrub vegetation such as *Calluna* are slow-growing and adapted to nutrient-poor environments, but the availability of resources was a likely driving force for any change, especially for invading plants (Hartley and Mitchell, 2005). The addition of nutrients, particularly nitrogen, shifts the grass: heather balance in favour of grasses (Aerts and Berendse, 1988, Hartley and Mitchell, 2005), hence the considerable potential for change observed in the vegetation (Table 6.4 and 6.5). This predisposition to invasion or succession (Gimingham, 1972, Bokdam and Gleichman, 2000) and the lack of controlled dunging investigations, only in upland or continental heaths (Vandenbos and Bakker, 1990 , Borghesio et al., 1999, Hartley and Mitchell, 2005), meant the findings were valuable for decision-making (e.g. for controlling animals numbers/type on vulnerable areas). The management implications are discussed later.

The research in this chapter extends the work of the few reviews of dunging impacts to lowland heath and provided experimental assessment (Bullock and Pakeman, 1997, Lake et al., 2001, Newton et al., 2009). Quantifying the impacts to the differing vegetation communities and habitats were central to meeting the overall research aims. Differential effects between habitats were illustrated by plant composition (Figs. 6.2, 6.3 and 6.4), sward height (Fig. 6.7), spatial heterogeneity and soil characteristics (Appendix 12). These portrayed the varying vegetation successional states and diverse communities of the lowland heath system (Grant and Armstrong, 1993, Bokdam, 2001). Some heathland studies have evaluated soil composition changes (Mitchell et al., 1999, Fottner et al., 2007) and the macronutrient assessment in this study indicated minimal changes in the relatively short period (Appendix 12), but was included within the analysis of covariance of grass cover (spatial heterogeneity) (Table 6.7).

Regression analysis of soil properties revealed that pH and phosphorus were predictors for variation in grass cover, indicating that dunging-related change may also be influential. Phosphorus is limiting for plant growth and available orthophosphate is rapidly depleted close to the plant roots (Richardson et al., 2009). It was possible that the recurrent dung deposition was likely to be important for vegetation response, depending on its availability in the dung and the microbial mobilization of this nutrient. Phosphorus availability is also influenced by pH (Richardson et al., 2009), so these factors should be analysed for correlation. Further analysis is required. Including those properties as covariates in the analysis validated their influence on the main factors (e.g. animal and worming factors) (Table 6.7) (research question iv) across habitats. Above-ground net primary productivity (ANPP) accounted for the differences between habitats (Begon et al., 1996, Gough et al., 2000) where nutrient cycling was an important mechanism and dunging was therefore pivotal (Hobbs, 1996, Gough et al., 2000); although soil moisture and organic matter are also influential (Hartley and Mitchell, 2005) but limitations meant they were not assessed.

6.4.4. Herbivore regime

Functional group composition, key species and sward height in woodland (Table 6.2, 6.3 and 6.4) indicated that nutrients were more available in cattle dung (i.e. higher sward and abundance) than horses (Figures 6.5 and 6.7). A higher proportion of diet is catabolised in ruminants (Sneddon and Argenzio, 1998) and further digestive breakdown may have meant more nutrients were available. This would have resulted in an elevated response to cattle dung. Chemical analysis of dung should be undertaken for future study; outlined later.

Worming regime differences (e.g. antihelmintics) may be important for vegetation response with significantly lower sward height and structure in wormed plots on mire (Table 6.4 and 6.5) (Fig. 6.7 and 6.8). In mire and wetland areas, where microbial activity and the mobilisation of nutrients that are available to plants are closely related to higher water levels (i.e. decomposition and nutrient cycling rates)(Jensen et al., 2003, Barker et al., 2004, UKREATE, 2010), the architectural and biological findings supported the retardation of dung degradation and therefore a reduction in available nutrients (Halley et al., 1989, Iglesias et al., 2006). A reduction in soil microbes and faecal arthropods delayed dung disappearance (Madsen et al., 1990, Sommer and Bibby, 2002, Suárez et al., 2003, Svedson et al., 2003) which was related to the rate of nutrient recycling (Borghesio et al., 1999, Bloor et al., 2012). The variable response in grassland and heath for architectural parameters (e.g. sward height, structure) were likely to be due to environmental factors (e.g. reduced soil moisture and decomposition rates compared to mire) (Beynon, 2012); functional group abundance remained mostly unchanged. Habitat-specific recommendations for worming regime may hold (e.g. excluding wormed stock from grassland), but other habitats should be further assessed (e.g. larger samples, faecal analysis). Any decisions about worming regime should also consider the respective herbivore, as differences in dung nutrient availabilities (Sneddon and Argenzio, 1998) were supported by the interaction between animal and worming regime for functional groups (Table 6.2), key species (Table 6.3) and grass cover (Table 6.6 and 6.7) in grassland and woodland.

Animal, dunging and worming regime are integral for making decisions about herbivore impacts and showed interacting effects indicating their influence on the vegetation on semi-natural habitats. Sward height changes based on these factors in grassland (Table 6.4) were explained by the habitat's high productivity dominated by graminaceous plants (Begon et al., 1996, Gough et al., 2000)(Figs. 6.3 and 6.6). Graminaceous plants showed their architectural and biological plasticity in all habitats (Table 6.3 and 6.4) (addressing research questions i and ii). A better understanding of their dynamics could assist in their control on conserved habitats and improve herbivore regimes (e.g. stabling cattle overnight to reduce inputs and limit sward growth).

6.4.5. Experimental limitations

There were unexpected findings and limitations in the study. The significant grass cover interaction for animal and worming within woodland (Table 6.7) highlighted the irregular patchy vegetation cover that existed in woodland. Although there was a distinct proportion of graminoids (Fig. 6.5), there was also sporadic other plants such as *Pteridium*. This plant was not evaluated in the spatial heterogeneity analysis as its fronds were absent from the ground cover assessment and it was removed from the key species analysis for its lone presence in woodlands. *Pteridium* may have altered other plant abundance by responding rapidly to nitrogen inputs (Gimingham, 1972), modifying the nutrient balance and shading out heathland plants (Mitchell et al., 1997, Marrs et al., 2007). An examination of other group cover would be more comprehensive, especially given the defecation behaviour observed in Chapter 3 in woodland. Experimental constraints and overall thesis aims (e.g. management of dominating grasses, prominent in all habitats), deemed the assessment appropriate for this lowland heath system and for application in other systems which suffer from dominating grasses (Britton et al., 2000b, Gordon et al., 2004, Kohler et al., 2004, Mitchell et al., 2008).

The large sample sizes of the structural complexity (n=9600) may have meant that differences were significant based on minimal variation, but this level of measurement was required in order to quantify the micro-scale variation brought about in the sward within each quadrat. This may also have been the reason that a distribution was non-normal and a generalized linear model was required.

Additionally, experimental limitations such as the size of the study site meant that the control and treatments were located adjacent to one another with a buffer rather than a separate plot design. It was possible that spill-over and edge effects could have contributed to the few differing vegetation responses observed for key species between wormed control and natural control plots (Appendix 15). The effect was only observed in very few cases mainly for the rapid-growing graminaceous species and longer-term evaluation may be more revealing for herbaceous plants and for the successional changes.

6.4.6. Importance of the findings

Heathland management of protected reserves using mixed grazing stock relies on a detailed quantification and understanding of those animals' impacts (Bokdam and Gleichman, 2000). It was clear from the findings presented here that dunging was a key mechanism for determining biological and architectural changes in the vegetation. The research has experimentally quantified the impact on the vegetation and revealed the complex relationships between the animal and vegetation for informing decisions, particularly for herbivore regimes which include antihelmintics. Parameters such as spatial heterogeneity expanded the knowledge of the grass: shrub mosaic on heathland which is of value for preventing the expansion of invasive plants such as *Molinia.* The study's findings also showed why it was important to separate dunging from the other mechanisms. However, it was fundamental to examine their effects comparatively to define the herbivore impacts on lowland heath sites and aid future management.

6.4.7. Implications for management

The findings indicated the value of quantifying the herbivore effects. Specific recommendations can be made based on this mechanism alone, with this herbivore regime and on this study site:

- Controlling graminoids on lowland heathlands, often a target of nature conservation and restoration, can be achieved by excluding animals from particularly sensitive vegetation communities. Based on the dunging mechanism findings alone, by controlling the amount of nutrient input to these areas through complete exclusion or reducing density, graminoid abundance will be limited and forbs will be maintained;

- Reducing dunging overall by the herbivores on *Molinia*-dominated habitats (e.g. lowering stocking densities further or limiting grazing time) would reduce its dominance. This plant showed significant increases in abundance and lateral growth due to dunging alone. Decisions should be made in balance with the other impact mechanisms;
- Removing the stock during certain periods (e.g. shoot establishment, March-April) or returning to traditional practices of stabling of cattle overnight (based on their behaviour of defecating when at rest) may limit sward growth and the related sward-density increase. Invertebrate assemblages may be impacted, but plant diversity will be enhanced by reducing competitive dominance of graminoids;
- Dominating graminaceous plants were hindered by animal-specific impacts and worming regime. Not accounting for knock-on effects to other taxon, employing horses alone (or reducing cattle) with a worming regime could reduce the abundance and cover of dominating grasses in grassland by retarding the degradation of dung. Long-term effects may differ as other ‘preferred’ plants (e.g. woody plants) will suffer the same fate;
- In other habitats such as mire, reducing or removing worming from herbivore regimes, may retain the structural heterogeneity (e.g. in mire) by improving faecal degradation (although this may contrast with a desire to reduce graminoids). Caution was taken for explicit recommendations based on structure as sample sizes meant significant differences were prevalent;
- The effect of worming and animal on woodland for grass cover means the exclusion of cattle from this specific habitat may be beneficial, if the objective is to control grasses in this habitat. Recommendations should account for site characteristics and conservation objectives.

Although some vegetation parameters may be affected by horses, and others by cattle, a low-level mixed regime remained important for generating the heterogeneity in the vegetation, not only for dunging but also for the other impact mechanisms previously evaluated. This final data chapter has completed the experimental evaluation of the large herbivores’ impacts to vegetation. It has also provided the evidence for general discussion (in Chapter 7) of the key findings based on the issues and research objectives raised in the introduction (Chapter 1). Overall recommendations are made at the end of the thesis.

Chapter 7

General discussion and conclusion

The studies that have formed the large part of this thesis have, for the first time, drawn together the main elements of herbivore impacts that influence the dynamics of lowland heath vegetation. The research has provided an in-depth assessment of herbivore activity as well as the individual mechanisms: herbage removal, trampling and dunging (research objectives 1 and 2). The experimental research has filled the gap in the subject knowledge which previously only reviewed the grazing practices and identified a lack of detailed experimental study.

In brief, the horses and cattle utilised their environments in very different ways and spatial-temporal trends varied primarily due to animal species, but there was overlap for particular habitat types and dietary selections. Herbage removal influenced vegetation community and architecture by reducing the sward structure and height, but spatial heterogeneity was maintained by the creation of gaps. Trampling decreased graminoid abundance and structure but did not reduce grass cover in the same way as herbage removal did. The indirect effects of dung deposition, which increased sward height and structural complexity with nutrient addition, were different in the wormed dung treatments, where dung degradation may have been impeded and vegetation did not respond in the same way.

It was clear that the activity and impacts of the herbivores were highly contributing to the changing dynamics of the vegetation. The overarching objective, to understand the multiple impacts of large herbivores upon lowland heath to meet biodiversity goals by improved grazing management, was only answered by an examination of all these mechanisms collectively. This discussion draws together the common themes that have become apparent through answering the research questions and three primary outcomes are discussed by asking, *what is the importance of the findings?* These three outcomes are that mixed grazing generated diverse effects, low-level stocking had a heterogeneous impact, and the separation of the impact mechanisms provided a clearer breakdown of their effects. Finally the implications for management and the wider nature conservation are discussed before the final conclusion.

7.1. Mixed regimes and sward heterogeneity

Mixed regimes are commonly employed in grazing management to meet wildlife conservation objectives (Grant et al., 1985, Gordon et al., 2004, EN, 2005, Critchley et al., 2008) and a complementary regime often adopts a combination horses and cattle (Menard et al., 2002, Loucougaray et al., 2004). The benefits of mixed grazing arise from differential body mass, digestive physiology and foraging strategies which generate heterogeneity between habitats and within the vegetation (Menard et al., 2002). The opening observational chapter (Chapter 3) described the differing spatial and temporal activities between the grazers, across the entire system, but also at the vegetation level. The variations in spatial and temporal activity corroborated with the findings of differential foraging strategies of horses and cattle (Menard et al., 2002, Lamoot et al., 2005) and had not previously been documented in lowland heath, only in upland areas (Hester and Baillie, 1998, Fraser et al., 2009). Indeed, the spatial and temporal patterns observed showed that the animal species (i.e. foraging strategy) was a determining factor for the changing patterns in vegetation, at a habitat scale in Chapter 3 but supported by the finer-scale effects on vegetation in later experimental chapters (Chapters 4, 5, 6). Activity also indicated additive effects of mixed grazing on vegetation (Ritchie and Olff, 1999, Loucougaray et al., 2004) generating a non-uniform sward due to a high overlap in selection for graminoids. There was also a compensatory effect due to differential diet due to digestive physiology and potential for competitive exclusion.

The recognition that mixed stocking produces species-rich and diverse swards has been widely reported for its benefits in conserved grasslands (van Wieren, 1995, Loucougaray et al., 2004). The short-cropping of swards by horses, the generation of latrine areas (usually taller avoided vegetation) and the compensatory effects by cattle (e.g. selecting woody plants) is valuable for plant diversity and heterogeneity (Loucougaray et al., 2004). The effects of mixed stocking were quantified within the experimental chapters, and demonstrated the diverse vegetation mosaic generated under such regimes. Herbage removal and trampling strongly influenced the abundance of graminoids, which is favourable for the establishment of other less competitive plants typical of heathlands, such as *Calluna* (Mitchell et al., 2008) and corresponds to the high selection for palatable and grazing tolerant grasses (Cran et al., 1997, Kimball and Schiffman, 2003). This was supported by the minimal impacts to the other functional groups, other than graminoids which were of high relative abundance. In contrast, long-term changes brought about by the mixed regime here could result in negative effects such as those seen in lowland heath and hard-grazed areas with decreased dwarf shrubs (e.g. *Calluna*) and an increase in graminoids (Bakker et al., 1983, Bullock and Pakeman, 1997). These studies did however recognise the importance of increasing gaps for heterogeneity, which was also exhibited here and may in the longer term increase species richness (i.e. through plant colonisation). The physical impacts of horses and cattle created variation in the vegetation due to their utilization of habitat and variable modification of vegetation, but indirect effects also generated heterogeneity due to dunging.

Much has been reported on the influence of dunging and nutrient input on heathland vegetation (Hartley and Mitchell, 2005, Fottner et al., 2007) although as identified in Chapter 1, few have evaluated the dunging effects of the mixed regimes (Critchley et al., 2008), especially on lowland heath (Barker et al., 2004). Differing digestion and foraging between horses and cattle result in differential dung nutrient availabilities, water content and degradability (Sneddon and Argenzio, 1998, Hongo and Akimoto, 2003). The resulting variability in vegetation response was evident in structure in Chapter 6, where increases in sward height enhanced structural heterogeneity based on plant density (Schwab et al., 2002, Hulme et al., 2003). Interacting underlying processes between animals and plants were also clearly identified from the impacts of dunging and the spatial-temporal activity, addressing the final research objective. Such processes were presented by the reduced effect of dung with a worming regime on structure and sward, due to the retardation of dung degradation (Halley et al., 1989, Iglesias et al., 2006), particularly in mire (animal ×worming regime). These findings indicated the diverse effects that mixed regimes have on the vegetation dynamics, especially on a sensitive and impoverished system like lowland heath (Gimingham, 1972, Borghesio et al., 1999) and indicate that low stocking rates are also important for these low nutrient systems.

The heterogeneity generated by mixed regimes is important for maintaining interrelationships between plants and other taxonomic groups such as avifauna (Evans et al., 2006), which for instance rely on a complex vegetation structure to support prey insects (Dennis et al., 2001). Indeed, consideration of the overall habitat arrangement is important in implementing grazing regimes, particularly on these sensitive areas, which are intimately related to the inhabiting fauna (Grant and Armstrong, 1993, Reid and

Hochuli, 2007). Heathland vegetation's dependence on continual grazing regimes (often mixed) should not be underestimated, as the animals play a complementary and additive role in shaping the vegetation (Ritchie and Olff, 1999, Bokdam, 2001). Retaining these critical diverse effects and ecological processes may only possible by implementation of low-density regimes simultaneously with mixed regimes (Vandenbos and Bakker, 1990 , Evans et al., 2006).

7.2. Low-stocking impacts

Extensive free-range grazing regimes, which are adopted for modern conservation management, have many of the characteristics of traditional grazing, particularly those on distant heaths (e.g. low stocking-density), practices which were less favoured in the last two centuries (Webb, 1998). The traditional approach allowed the animals to maintain themselves on less favourable but expansive lands and were often left out all year round (Lake et al., 2001) as were the animals in this study. A return to these approaches has been observed in other extensive grazing systems with stocking densities around 0.2-0.8 livestock units per hectare (Hodder et al., 2005). The low-stocking regime within this study had a stocking density of exactly 0.2 LU/ha for all grazing animals and generated variable vegetation effects across the system. At a landscape scale the utilization of habitats was variable, generated by a high selectivity by this low-stocking density.

The vegetation response was also variable at low stocking rates through factors such as differential growth, damage or removal (Bokdam, 2001). Indeed, these responses were directly determined by the physical mechanisms of herbage removal and trampling, generating variable patterns of structural complexity. The responses were also based upon each habitat's sensitivity to large herbivore impacts (Milchunas and Lauenroth, 1993), the habitat's vegetation composition and how each habitat is differentially selected (Chapter 3). The reduced structural complexity generated by herbage removal and trampling at Eelmoor was contrary to other studies (Olff and Ritchie, 1998, Mouissie et al., 2008) and experimental studies of low-stocking effects on fertile grasslands (Scimone et al., 2007). These contrasting findings were attributed to high canopy density and sward height reduction as exhibited in tall angiosperms (Schwab et al., 2002) but possibly the variability in vegetation between each habitat using the same sampling methods. This variability between habitats and the possible weakness by using the same sampling method is unlikely as the work by Buttler (1992) measured the plant structure within a similar complex habitat system (Buttler, 1992). Moreover, the ecological attributes of lowland heath were likely to be contributory factors, because of the nutrient poor soils, reduced primary productivity and vulnerability to nitrification (Gimingham, 1972, Aerts and Berendse, 1989, van Vuuren et al., 1992).

Low utilization levels on upland moorland are a practical solution to avoid degradation of the vegetation (Pakeman and Nolan, 2009), a particular problem with over-stocked sites and high trampling pressures (Hulme et al., 2003, Pakeman et al., 2003). The low animal levels at Eelmoor had effects on the vegetation through trampling, reducing structural heterogeneity and sward height on all habitats, and there were no major issues with soil degradation, other than variable compaction through habitat use. These focussed trampling effects on highly-selected areas (e.g. grassland) was evident by the soil compaction data and trampling intensities (Table 5.1 and 5.9), but no relationship of soil compaction with grass cover was evident. Interestingly, trampling effects have been shown to be detrimental at low intensities on other heath systems, more so than herbage removal in some upland habitat (Hester and Baillie, 1998). The low-density regime and the abundance of graminoids in the sward may contribute to the minimal impact observed.

The control of grasses at low stocking densities may be difficult, given their ability for lateral growth, with graminoids being less impacted by trampling (Augustine and McNaughton, 1998, Hartley and Mitchell, 2005). Conservation objectives are usually targeted at controlling invasive grasses and while herbage removal and trampling reduced abundance of grasses in grassland, mire and woodland, the effect was not as well defined on heath in this research. The effects on grass cover are also less clear: trampling had the effect of increasing grass cover in grassland and woodland, while dunging had no discernible effect in any habitat, other than an interaction of worming and treatment in grassland. The changing dynamics of grass in a patch are likely to be attributed to the increased nutrient levels (Hartley and Mitchell, 2005), the existing seed bank as well as the spatial distribution of the vegetation and its composition (Hester and Baillie, 1998).

7.3. Disaggregating the impact mechanisms

Separating the impact mechanisms (herbage removal, trampling and grazing) into individual assessments of vegetation change allowed a comprehensive representation of herbivore effects. The few studies that had identified the importance of assessing the complex mechanisms separately (Kohler et al., 2004, Rook et al., 2004, Oom et al., 2008) had not experimentally tested non-simulated vegetation changes or examined mixed grazing impacts on lowland heath. The impact mechanisms had differing effects on the same habitats for functional group composition, for example. Quantifying the actual effects of these mechanisms in an extensively-grazed system also meant the underlying dynamics could be identified (research objective 3) and generated some valuable insights. For instance, the vegetation change as a result of worming regime was unexpected, and partially revealed the underlying processes within the ecosystem, such as the retardation of dung degradation (Halley et al., 1989, Iglesias et al., 2006). Overall, examination of the mechanisms separately, but then collectively reviewing and discussing the findings in one piece of research is a novel approach for lowland heath, where conservation grazing is often employed (Bullock and Pakeman, 1997, Newton et al., 2009). On these habitats the lack of evidence-based decisions, e.g. over- or under-grazing, can have repercussions for the vulnerable biodiversity (Bardgett et al., 1995, Welch and Scott, 1995, Lake et al., 2001).

Making an empirical assessment of changing vegetation can be challenging in the field and often simulated effects are substituted into the experimental design. Simulations of the impacts of large herbivores have been previously carried out by clipping or mowing the vegetation (Barker et al., 2004, Kohler et al., 2006a), trampling with artificial hooves (Kobayashi et al., 1997, Kohler et al., 2004), or simulated dunging or manuring (Gough et al., 2000, Kohler et al., 2005). The non-simulated approach for herbage removal and trampling within this study has revealed patterns such as vegetation shifts (e.g. grass cover decreased in grazed plots and increased in some trampled plots). These differing effects are suggested to be related to mandibular removal versus compression effects (Cole, 1995a, Hongo and Akimoto, 2003), the latter favouring lateral growth and therefore resulting in increased grass cover (Mitchell et al., 2008).

The subtle differences contribute to larger trends in the landscape, e.g. successional vegetation shifts, effects that would be lost through a simple assessment of a measure of all-encompassing ‘grazing’. The individual examinations also developed the methods for grazing managers to make more detailed vegetation assessments of livestock effects and provide early indications of negative grazing impacts (e.g. grass invasion examined by cover).

The research as a whole had similarities with the management-orientated work by Kohler and co-workers (2006) in the Swiss Jura Mountains. Their work made examinations of the impact mechanisms on the vegetation and also the spatial and seasonal patterns (Kohler et al., 2006b). In this thesis, the steps made towards understanding these spatial and temporal trends and then examining the component impacts are valuable for the management of highly heterogeneous landscapes. This is because they deliver a more accurate understanding of what is occurring which can support decisions at a management level. By understanding the fine-scale changes as well as the broader-scale issues, evidence-based recommendations for grazing management can be implemented. The approaches documented in this thesis are applicable to other semi-natural terrestrial systems with a heterogeneous landscape and similar conservation objectives.

7.4. Implications for grazing management

7.4.1 Restoring grazing function

The intimate connection that lowland heath had, and still has, with grazing has meant that the declines in extensive grazing across the UK have exacerbated the declines in the habitat (Bullock and Pakeman, 1997, Webb, 1998). Re-introduction of management of these systems by mixed grazing has been undertaken in an effort to cease or reverse the declines. Utilising low-density mixed regimes, as were commonly adopted in lowland heath systems across lowland Europe (Webb, 1998, Lake et al., 2001) has been considered instrumental in maintaining lowland heath in favourable conservation status (Lake et al., 2001). The work in this thesis has recognised the important factors for reinstating grazing on lowland heathland systems (i.e. particular grazing regime) also identified by other key reviews (Bullock and Pakeman, 1997, Lake et al., 2001), but goes further by quantifying the impacts on vegetation by these influential animals. In general, it is suggested from this work that mixed low-density grazing on lowland heath can be highly beneficial for reducing graminoids through herbage removal, creating gaps in the sward by trampling and creating structural heterogeneity through patchy dunging effects. These effects restore the ecological processes which have disappeared in many small protected areas where traditional grazing has ceased, and reinstated the trophic function of these systems.

7.4.2. Overarching benefits

There has been some controversy about the benefits of introducing herbivores for lowland heath management, for instance regarding the shifting heath: grass dynamic which is often observed in overgrazed systems (Hester and Baillie, 1998). Additionally the effect on invertebrate and vertebrate communities through detrimental changes to vegetation structure has been reported (Dennis, 1998, Offer et al., 2003). The negative effects include the nutrient enrichment of some impoverished habitat through redistribution of dung. The subsequent grass invasion does support the opinion against the use of grazers with a shifting grass dominance (Hester and Baillie, 1998, Cosyns et al., 2005), although there is evidence that ungrazed tussocks support higher invertebrate abundances, e.g. spiders (Dennis et al., 2001). Overall, the gap creation, removal of graminoids and a reduction in sward height generated more heterogeneity in the vegetation and habitat than excluded controls, despite the structural findings. Although the impacts may be more apparent in habitats that received higher selection by the animals (e.g. grassland), quantifiable effects were generated in the other habitats (e.g. mire). Overall, the diverse effects from the low-density mixed regime were beneficial for the ongoing management of the lowland heath system at Eelmoor. The research has delivered or contributed to the conservation aims of this site, namely to: (i) maintain, increase and enhance valued habitats; (ii) maintain or increase populations of valued species; and (iii) control, reduce or remove alien and invasive species (Hall et al., 2009).

7.4.3. Enhancing the knowledge and decision-making

A non-empirical approach to grazing management on sensitive systems like lowland heath can lead to highly variable or undesirable impacts as noted in the review by Lake et al. (2001). These impacts may be adverse based on inappropriate decisions. The controversial issue of introducing stock onto heaths, as identified in the review by Newton et al. (2009) and the lack of experimental evidence of their impacts, was a motivation for this research. In addition, the opinions of lowland heath managers when making grazing regime decisions are often based on expert knowledge, which is invaluable (Newton et al., 2009). Marrying these opinions with scientific evidence has been a key focus for quantifying the actual impacts in this research. There has been consensus between these expert opinions and the observational-based studies, but a lack of experimental assessments has meant it is difficult to weigh up if a similar consensus exists (Newton et al., 2009). The work here addressed that void, albeit in the context of one mixed regime in a single diverse site.

Experimentally, and observationally, quantifying the effects of herbivores at Eelmoor has improved the understanding of using these animals for lowland heath management (research objective 3). The research has extended the existing evidence for spatial and temporal patterns on heathlands (Hester and Baillie, 1998, Oom et al., 2008) and developed the experimental approach of assessing grazing management effects. The comprehensive quantification on this site has meant managers can begin to utilise experimental data for decisions about their stock at a vegetation level as well as at the landscape scale. As noted in Lake et al. (2001) site characteristics, livestock type, grazing season and climate are important factors for designing grazing regimes, but collating the separate impacts on this priority habitat validates the decisions being made. The importance for making the most informed judgments is demonstrated by the statutory protections and UK Biodiversity Action Plan placed on this habitat type to cease or reverse the declines in biodiversity (DOE, 1995). Some general recommendations can be made from the work in this thesis for wider grazing management.

7.5. Grazing management recommendations for lowland heath

A number of general recommendations from the overall assessment of activity and impact mechanisms can be made based on this lowland heath site and regime, particularly focussed on the control of graminaceous plants:-

1. Mixed horse and cattle grazing should be used as a tool for biomass removal in grass-rich lowland heath habitats because of their compensatory and additive effects spatially and temporally;

2. A low stocking regime can effectively control graminoid abundance and sward height through herbage removal and trampling, and therefore should be maintained at such stocking densities to avoid overgrazing or degradation of habitat;
3. In grass-rich habitats excessive trampling should be avoided as this mechanism will promote lateral prostrate grass growth and enhance its cover;
4. Excluding animals from vulnerable habitats (e.g. grassland, heath and mire), reducing time spent occupying those habitats, or indeed returning to traditional methods of overnight stabling (for cattle) would limit the redistribution of nutrient from richer sources to nutrient-poor habitats and limit the spread of graminoids;
5. Removing antihelmintics from herbivore regimes in wetland mire habitats only (worming effects were inconclusive in other habitats) would improve faecal degradation and retain or enhance structure of dense tussocked vegetation; this may conflict with a desired reduction in graminoids however;
6. A low-density mixed regime of horses and cattle should be employed for generating overall vegetation heterogeneity (architectural and biological) in the sward at the micro-scale;

Recommendations based on worming regime could not be explicitly made for other habitats due to the variable nature of the findings across those habitats. Further work should be undertaken (see below). In each chapter recommendations have also been provided.

7.6. Practical nature conservation

Evidence-based practical conservation brings together the functional approach needed to manage the large and often complex systems with scientific validation, as it has done in this research. Protected area management is of considerable benefit for providing a refuge for species, especially those that are expanding their range in a changing climate (Thomas et al., 2012). In addition, restoring habitats at a broad scale is an internationally-adopted approach that re-establishes the original species or communities through targeted community or ecosystem conservation (Begon et al., 1996, Pfadenhauer and Grootjans, 1999, Griscom and Ashton, 2011). Ecological restoration, using large herbivores on protected reserves, may be applicable to an array of habitats, particularly lowland temperate ecosystems. The conservation of lowland heath relies on this type of practical restoration because of its reliance on continual management and the declines observed in recent history. The loss of lowland heath in the last 200 years has been dramatic, owing to the threats outlined in the Chapter 1 such as changing agricultural practices, degradation through eutrophication, and the cessation of traditional practices (Webb, 1990). The broad conservation practices employed on this habitat can re-establish the original communities by reinstating the processes which governed them. Therefore, reintroducing large herbivores in an effort to restore such processes should be a practical conservation approach for these habitats.

7.7. Reversing the declines in habitat loss and biodiversity

In a world with a growing human population and species extinction rates far exceeding the background rate (Butchart et al., 2010), there appears to be little sign of slowing the declines in habitat. Changing land use, which has been observed to be the primary factor for future habitat and overall biodiversity loss (Sala et al., 2000), continue to be observed at an alarming rate. A wider conservation effort has been established on a global scale, hence the Aichi Biodiversity Targets within the Strategic Plan for Biodiversity 2011-2020 (SCBD, 2013), but at this moment in time these large-scale efforts may be difficult to implement. Only time will tell if these targets are met. More localised efforts are being made to cease or reverse declines at a regional or national level, making significant steps towards conservation management of semi-natural habitats. The conservation success stories, such as the improvement in ‘condition’ based on Natural England’s Condition Assessments of Sites of Scientific Interest (NE, 2008), or the increasing use of protected reserves by threatened species (Thomas et al., 2012), many of which are managed with grazing regimes, provide a mechanism for larger-scale conservation to be addressed. Such large-scale conservation has been considered and encouraged in the review of England’s wildlife sites and the ‘coherent and resilient’ ecological network that they can create (Lawton et al., 2010). Therefore, if there is local site-level success, then these successes add to the broader scale conservation efforts, which can address or reverse some of the declines in biodiversity.

Enhancing evidence-based conservation is crucial for extending the scientific knowledge of conserving biodiversity. The lack of this knowledge was recognised in the Global Biodiversity Assessment and the UN Millennium Ecosystem Assessment (Heywood, 1993, Powledge, 2006), following the Convention on Biological Diversity (1993).

Improving baseline monitoring, especially for priority habitats such as lowland heath, will not only enhance the knowledge for on-the-ground managers, but it may also increase ecological knowledge to prevent further biodiversity loss in these, and other, priority habitats.

7.8. Limitations of the research

The experimental study was designed in such a way to accommodate the naturally-occurring impacts on this system. In order to quantify the actual impacts of herbage removal and trampling, in a non-simulated manner, the factors could not be separated completely from one another. For herbage removal plots it was not possible to entirely control the effects of trampling, but the experimental plots were located within foraging habitat and not transient trampled areas, which was important to capture the grazing variability. The minimal dung that was deposited was removed immediately. In the trampling plots, grazing was minimised as their location was adjacent to foraging habitats on transient areas, while camera-trapping data confirmed that grazing was minimal. The design incorporated simulated dunging, diluted and applied homogeneously across the plots. This unfortunately may not have allowed the natural degradation process of dung-piles to act out as the dung mixtures were diluted for even application.

In the experimental chapters, constraints on the study meant that only three replicate blocks for each of the four habitats could be assessed (each containing a minimum six sampled plots within, twelve sampled plots for dunging). Although the blocks across all habitats represented the variability in vegetation across the 79 hectare site, increasing this number per habitat may have been more statistically powerful.

Scale was a limitation of the research as the fine-scale measurements of the vegetation unfortunately meant logistically it was not feasible to study the effects over more than one site and for more than one regime (mixed low-density). The diverse nature of the site and the common characteristics shared with other lowland heath sites meant the vegetation communities were typical of many systems across Southern England, but making wider conclusions has to be undertaken with caution and also mindful of particular site features.

7.9. Recommended further work

The research within this thesis has focussed on two scales of investigation, the landscape scale and vegetation scale, which are most appropriate for the management recommendations of herbivore-managed sites. These two scales have allowed accurate quantification of the impacts over the research duration. However, the potential scope of investigation is wider than those documented here. Incorporating multiple sites within southern England would shed more light on varied low-stocking regimes and animal types, to enhance the knowledge for conserving this priority habitat. In addition, incorporating the NVC communities or sub-communities (detailed in Chapter 2) rather than the broad habitat assemblages would be beneficial for measuring the impact on key botany.

The benefit of evaluating the broad habitats however is that it may allow a rapid assessment method of herbivore impacts, examining parameters such as spatial heterogeneity (e.g. grass cover) and sward height which were shown to be appropriate measures of vertical and horizontal vegetation change. This method could be suited for site managers who need to make rapid but empirically-supported decisions. Furthermore, the opening data chapter also generated an approach for gaining an initial assessment of spatial and temporal activity at a landscape scale. Expanding the scope of this work by incorporating a spatially-explicit model with the vegetation impact assessments would provide an accessible method for managers to quantify impact across the site, similar to the work undertaken in mountain wooded pasture (Kohler et al., 2006b). Lowland heath is however a much more heterogeneous landscape than the pasture investigated by Kohler et al. (2004; 2006), and the impacts on vegetation were at a finer scale within in this study.

The interactions of worming regime displayed variable vegetation responses for the parameters between habitats (e.g. decreased height in mire, increased height in grassland). Further evaluation of the impacts of worming regime on plants should be undertaken in an effort to quantify and explain these differences before recommendations can be made. The complex relationships between the vegetation and other taxonomic groups, in particular invertebrates, should be an area of further work in this field. The studies that have examined grazing-induced structural heterogeneity and invertebrate communities on lowland heathland and grassland (Dennis et al., 1997, Dennis et al., 2001, Offer et al., 2003, Schaffers et al., 2008) identify the importance of grazing in supporting these populations. The knock-on effects of grazing on other assemblages (e.g. avifauna, reptiles) are seen in many wildlife conservation areas and are often negative (Lake et al., 2001). Examining these effects may begin to bridge the gap between the many conflicting grazing opinions (Lake et al., 2001).

7.10. Conclusion

The adoption of large herbivores to meet conservation objectives on semi-natural habitats is widespread, based on the presumption of grazing-induced heterogeneity and conservation of biological diversity. Adopting these regimes is prevalent in habitats that were traditionally maintained by such regimes, for instance lowland heath where dominating grasses have become prevalent. The outcome of induced-heterogeneity is not assured and often habitat degradation may be the result. If these management options are to be successful in restoring ecological processes and conserving vulnerable habitats such as lowland heath, then they must be based on empirically-derived data.

In order to mitigate the threats to habitat and species, meet the conservation objectives set out for these systems, and measure the influence of herbivores on the vegetation, the impacts must be quantified and the factors integrated into grazing management. This research has been successful in evaluating the multiple impacts of large herbivores upon a lowland heath system, assessing the animals and the vegetation within grassland, mire, heath and woodland sub-habitats. This addressed the overall research aim. By undertaking this evaluation, research objectives 1 and 2, the work has also identified the factors which are important for integration into grazing management. These include the grazing regime, the complex of habitats, the impact mechanisms as well as the site characteristics, which are important to comprehensively quantify the herbivore effects.

Experimental assessment at this level has been not been carried out within lowland heath previously, as recognised by Newton et al. (2009). The work in this thesis extends the knowledge and goes further than the previous reviews and studies, which identified the factors responsible for designing a grazing regime and individually-assessed each impact mechanism. The study provides the experimental evidence needed to partner the decisions for grazing management and offers a comprehensive approach for managers for quantifying grazing impacts on lowland heath, and therefore specifically addressed research objective 3.

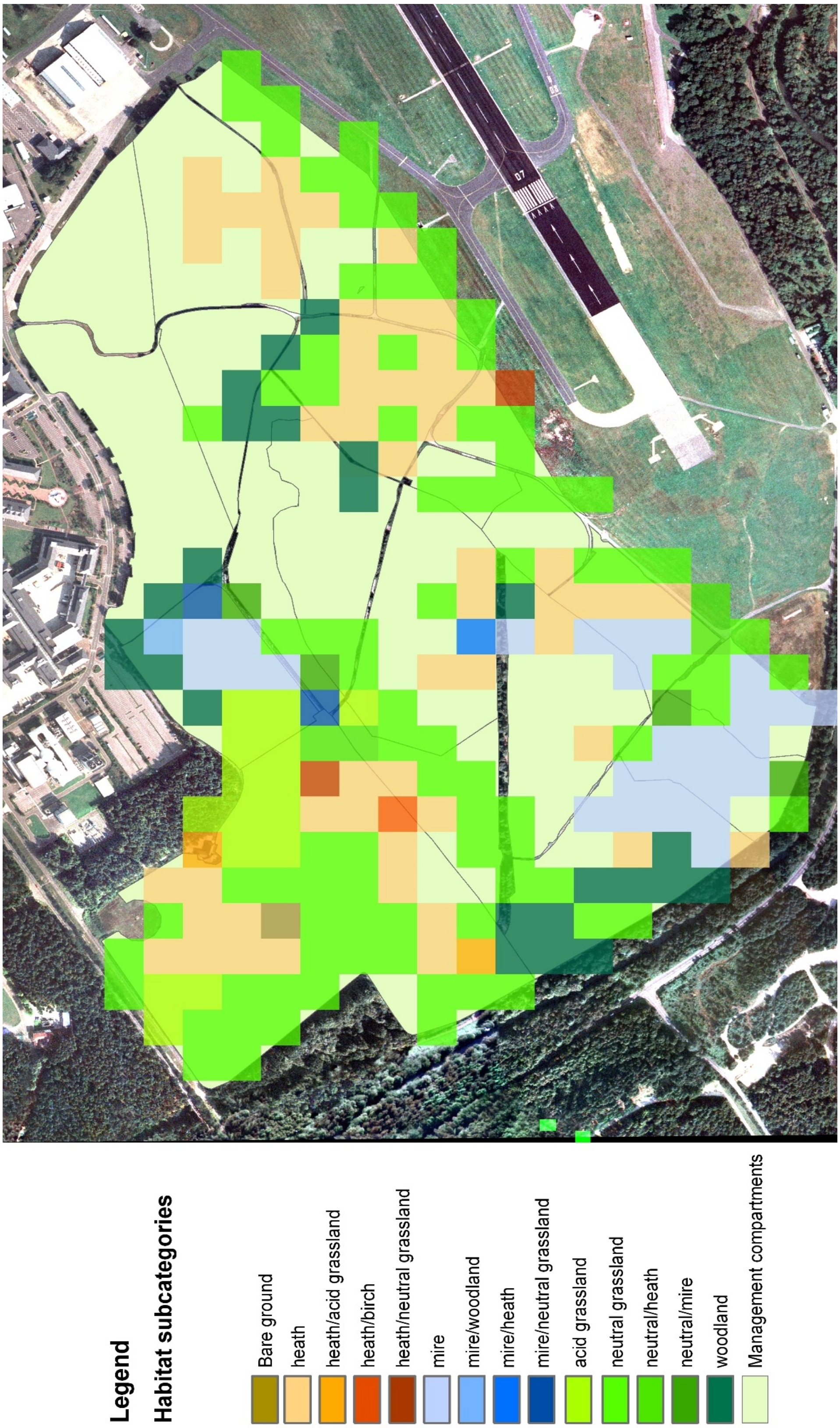
The use of grazing management for controlling dominating grasses, creating colonising gaps and enhancing structural complexity, as well as identifying the possible effects of antihelmintics is important for future restoration and biodiversity goals, which addressed the final part of the research aim. The findings may begin to resolve some controversies over the effects on biological diversity and provides a basis for further work on this valuable habitat and internationally-adopted grazing management strategy.

Appendix 1

Aerial photograph of Eelmoor Marsh SSSI 2000. Copyright Getmapping 2012.

Appendix 2

Habitat sub-categories for occupied grid locations of horses and cattle on the study site. Raster image overlaid on aerial image of Eelmoor Marsh SSSI. Copyright Getmapping 2012.



Appendix 3

Key vascular plant species of Eelmoor Marsh Site of Special Scientific Interest (SSSI) (Hall et al., 2009)

Species	**Common name**
Carex hostiana	Tawny sedge
Centaurium pulchellum	Lesser centaury
Cuscuta epithymum	Common dodder
Dactylorhiza incarnata pulchella	Early marsh orchid
Dactylorhiza praetermissa	Southern marsh orchid
Epipactis palustris	Marsh helleborine
Epipactis phyllanthes	Green-flowered helleborine
Filago vulgaris	Common cudweed
Filipendula vulgaris	Dropwort
Galium parisiense	Wall bedstraw
Genista anglica	Petty whin
Hypericum elodes	Bog St. John’s wort
Isolepsis fluitans	Floating club-rush
Moenchia erecta	Upright chickweed
Ophioglossum vulgatum	Adder’s-tongue fern
Oreopteris limbosperma	Lemon-scented fern
Parentucellia viscosa	Yellow bartsia
Pinguicula vulgaris	Common / Purple butterwort
Pyrola minor	Wintergreen
Rhynchospora alba	White beak-sedge
Stellaria pallida	Pale chickweed
Trifolium ornithopodioides	Fenugreek / Bird's-foot clover
Trifolium striatum	Knotted clover
Utricularia australis	Greater bladderwort
Utricularia minor	Lesser bladderwort

Appendix 4

Pooled soil chemical composition for each habitat type, initial detailed assessment of Phosphorus, Potassium, Magnesium, Total Nitrogen, and Organic Carbon. Analysed and results produced by Natural Resources Management Laboratories Ltd, Berkshire, UK.

		Grassland	Mire	Woodland	Heath
pH		5.7	4.8	4.1	4.2
Available Phosphorus	mg/l	15	7	5	7
Available Potassium	mg/l	70	71	98	67
Available Magnesium	mg/l	43	68	39	39
Total Nitrogen	% w/w	0.17	0.53	0.25	0.17
Organic Carbon by Wet Oxidation	% w/w	2.2	6.3	6.4	6.4

Appendix 5

Sample vegetation parameter recoding sheet for dunging plots

															WORMED TREATMENT							
Wood 1	laffan woods		Horse																Cattle			
			C		T		C		T		C		T		C		T		C		T	
Sward	**H(cm)**	H1	43.1		14.2		18.9		1.4		22.4		29.1		61.1		3.1		25.4		44.1	
Height		H2	10.2		27.6		59.3		44.4		31.2		6.5		10.2		4.9		44.4		66.2	
		H3	29.5		11.4		21.7		11		13.5		2.9		2.3		48.2		21.9		28.5	
		H4	64.4		36.2		33.2		0.9		6.5		3.2		2.6		13		18.4		45.6	
		H5	0.6		25.6		16.3		32.8		18.4		35.7		1.9		43.4		2.7		25.5	
		H6	56.7		59.6		14.1		23.8		20.4		4.1		3.2		4.1		18.5		25	
		H7	19.1		28.4		12.1		22.8		11.7		1.9		13.5		0.4		2.4		50.2	
		H8	63.2		39.6		54.3		38.5		9.4		15.3		66.2		3.4		30.2		67.2	
		MEAN	35.85		30.33		28.74		21.95		16.69		12.34		20.13		15.06		20.49		44.04	
				SP.		SP.		SP.		SP.		SP.		SP.		SP.		SP.		SP.		SP.
Str_hetero	**P (no. point intercepts)**	P1	2	bracken	1	bracken	2	bramble	1	bramble	2	bracken	1	poa	0		0		0		2	bracken
		P2	0		0		2	bramble	1	bramble	3	bracken	1	bramble	1	bracken	1	bramble	0		1	poa
		P3	3	bracken	0		1	bramble	0		3	bracken	1	poa	2	bramble	1	bramble	0		1	poa
		P4	2	poa	0		0		1	bramble	4	bracken	2	bramble	1	bramble	2	bracken	0		2	poa
		P5	2	bracken	1	bramble	0		2	willow	4	bramble	1	bramble	1	bramble	2	bracken	2	poa	2	poa
		P6	2	bracken	1	bracken	2	bracken	1	bramble	4	bramble	2	bramble	2	bracken	1	bramble	0		1	bramble
		P7	0		0		2	bramble	1	bracken	2	bracken	1	poa	1	bracken	1	bramble	0		2	bramble
		P8	3	poa	1	bramble	0		1	bramble	2	bramble	1	bramble	1	bramble	1	bramble	0		2	bramble
		-	3	poa	1	bramble	1	bramble	0		5	bracken	2	bramble	1	bracken	2	bracken	0		2	poa
		-	0		1	bracken	2	bramble	0		3	bracken	1	poa	0		2	bracken	1	bracken	3	poa
		-	1	poa	0	bramble	0		0	bramble	3	bramble	0		0		1	bramble	1	poa	1	poa
		-	0		1	bramble	2	bramble	0		3	bramble	0		0		1	bramble	1	poa	2	poa
		-	1	bramble	1	bramble	2	bramble	1	bracken	4	poa	1	bracken	0		0		2	poa	2	poa
		-	1	poa	0		2	bracken	1	bramble	6	bramble	2	bramble	0		0		2	bramble	3	bracken
		-	2	poa	1	bracken	3	bramble	0		2	bracken	1	bracken	0		1	bramble	2	poa	2	poa
		-	1	bramble	1	bramble	2	bramble	1	bramble	0		0		0		1	bramble	0		2	bracken
		-	0		1	bracken	1	bracken	1	bramble	1	bracken	2	willow	1	poa	0		1	poa	2	bramble
		P97	0		0		1	bramble	1	bramble	3	poa	1	poa	1	poa	0		2	poa	2	poa
		P98	2	bracken	3	bramble	2	bramble	0		2	bracken	1	bramble	0		0		2	poa	3	bracken
		P99	2	bramble	2	bramble	1	bracken	1	bramble	2	bramble	0		0		1	bramble	2	poa	2	poa
		P100	1	poa	2	bramble	1	bramble	1	bramble	2	bramble	0		1	pine	1	bramble	1	poa	1	poa
	Max height canopy (cm)		88.7		54.1		64.3		69.5		41.3		61.2		76.9		57.8		63.4		98.8	
Qual. Structural	**Plant cover (%) (<20cm)**		17		71		54		42		59		58		53		47		39		76	
	Plant cover (%)(21-60cm)		58		26		38		55		37		38		45		52		60		23	
	Plant cover (%) (>60cm)		5		3		8		3		4		4		2		1		1		1	
	Plant biomass (<20cm)		9		62		53		46		28		39		17		25		58		92	
	Plant biomass (21-60cm)		54		27		33		36		51		45		71		70		39		7	
	Plant biomass (>60cm)		18		11		14		18		21		16		12		5		3		<1	
Spatial heterogeneity	**Total plant**		38		73		76		85		89		59		38		36		94		91	
	(O1) Other																					
	Gap	O1	4		20		15		6		4		0		0		0		8		0	
	Moss	O2	1		0		0		0		0		0		0		1		<1		0	
	Litter	O3	57		7		19		9		16		41		72		63		11		1	
	Other (stones,	O4	0		0		0		0		0		0		0		0		0		8	
	Fucntional group cover (%)																					
	Herb	F1	6		11		5		6		3		0		0		0		1		1	
	Grass	F2	9		9		4		2		7		12		19		0		94		95	
	Legume	F3	0		0		0		0		0		0		0		0		0		0	
	Other	F4	85		80		91		92		90		88		81		100		5		4	

Appendix 6

Non-metric multidimensional scaling species abundance data for herbage removal. (G=GRASSLAND, H=HEATH, M=MIRE, W=WOODLAND; 1-3= replicate block; C=CONTROL, T=TREATMENT)

		Agrostis	*Rubus*	*Juncus*	*Carex*	*Festuca*	*Ulex*	*Molinia*	*E.tetralix*	*Luzula*	*Pteridium*
G1	C	1	0	5	14	10	0	42	0	0	0
	C	55	0	1	3	0	0	0	0	0	0
	C	57	0	3	10	1	0	13	0	0	0
	C	39	0	3	8	1	0	35	0	0	0
	C	49	0	4	6	0	0	8	0	0	0
	C	37	0	6	13	0	0	18	0	0	0
	T	33	0	0	1	0	0	0	0	0	0
	T	39	0	0	1	0	0	1	0	0	0
	T	45	0	0	1	0	0	1	0	0	0
	T	39	0	0	0	0	0	3	0	0	0
	T	39	0	2	2	0	0	2	0	0	0
	T	54	0	0	2	4	0	3	0	0	0
G2	C	2	0	0	0	0	0	1	0	0	0
	C	14	0	0	0	0	0	0	0	0	0
	C	31	0	0	0	0	0	0	0	0	0
	C	8	0	0	0	0	0	0	0	0	0
	C	34	0	0	0	0	0	0	0	0	0
	C	35	0	0	0	0	0	0	0	0	0
	T	41	0	3	0	7	0	2	0	0	0
	T	37	0	3	1	5	0	0	0	0	0
	T	42	0	0	0	7	0	0	0	0	0
	T	25	0	0	2	11	0	14	0	0	0
	T	43	0	0	0	6	0	0	0	0	0
	T	36	0	0	0	1	0	0	0	0	0
G3	C	16	0	0	7	2	0	43	0	0	0
	C	23	0	3	15	2	0	41	0	0	0
	C	29	0	4	18	0	0	32	0	0	0
	C	29	0	1	16	4	0	29	0	0	0
	C	24	0	0	12	6	0	41	0	0	0
	C	28	0	1	6	8	0	41	0	0	0
	T	35	0	1	3	0	0	11	0	0	0
	T	31	0	0	1	0	0	12	0	0	0
	T	29	0	0	3	0	0	8	0	0	0
	T	28	0	0	1	0	0	2	0	0	0
	T	14	0	2	3	7	0	8	0	0	0
	T	9	0	4	3	9	0	15	0	0	0
H1	C	0	0	0	26	0	0	12	29	0	0
	C	0	0	0	18	0	0	32	9	0	0
	C	0	0	0	23	0	0	36	7	0	0
	C	0	0	0	33	0	0	16	19	0	0
	C	0	0	0	15	0	0	27	20	0	0
	C	0	0	0	26	0	0	7	37	0	0
	T	0	0	0	2	0	0	27	13	0	0
	T	0	0	0	11	0	0	41	6	0	0
	T	0	0	0	9	0	0	32	11	0	0
	T	0	0	0	6	0	0	36	13	0	0
	T	14	0	0	17	3	0	23	5	3	0
	T	10	0	0	15	5	0	39	10	0	0
H2	C	10	0	6	10	5	0	6	5	0	0
	C	1	0	5	6	1	0	3	13	0	0
	C	4	0	2	14	5	0	4	9	0	0
	C	7	0	13	6	7	0	10	7	0	0
	C	1	0	0	0	4	0	10	22	5	0
	C	13	0	0	4	4	0	21	5	0	0
	T	8	0	2	15	0	0	10	6	0	0
	T	0	0	4	14	0	0	10	6	0	0
	T	2	0	0	5	0	0	5	15	0	0
	T	1	0	0	23	0	0	7	17	0	0
	T	10	0	7	9	4	0	9	8	0	0
	T	3	0	0	21	4	0	11	15	0	0
H3	C	11	0	0	10	7	0	20	7	0	0
	C	1	0	1	12	3	0	4	23	0	0
	C	3	0	1	17	4	0	25	12	1	0
	C	4	0	0	4	13	0	4	18	0	0
	C	1	0	5	15	6	0	25	13	0	0
	C	12	0	1	16	10	0	31	5	0	0
	T	18	0	5	6	1	0	31	12	1	0
	T	11	0	0	13	3	0	19	9	0	0
	T	4	0	0	10	9	0	27	5	0	0
	T	1	0	2	5	12	0	25	7	1	0
	T	5	0	1	7	10	0	27	8	0	0
	T	1	0	1	8	2	0	39	14	0	0

Appendix 6 continued

	Calluna	*Plantago*	*Holcus*	*Geranium*	*Potentilla reptans*	*Ranunculus repens*	*Ranunculus acris*	*Trifolium*	*Salix*	*Centurea*
G1	0	0	13	0	0	0	0	0	0	0
	0	0	7	0	0	0	0	0	0	0
	0	0	1	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	1	0	0	0	0	0	26
	0	0	0	0	0	0	3	0	0	9
	0	0	0	0	0	0	0	0	25	0
	0	1	0	0	0	34	2	1	0	0
	0	0	0	0	0	14	0	0	0	0
	0	6	0	0	0	15	4	0	0	1
	0	1	0	0	0	7	2	0	15	1
	0	0	1	0	0	0	3	0	8	1
G2	0	40	14	0	0	0	3	5	0	0
	0	16	10	0	0	0	3	0	0	0
	0	12	8	0	0	0	1	0	0	0
	0	29	2	2	0	0	2	0	0	0
	0	16	1	0	0	0	12	1	0	0
	0	18	0	0	0	0	4	0	0	5
	0	0	0	0	0	8	2	0	0	0
	0	0	0	0	0	13	0	0	0	0
	0	3	0	0	0	0	7	1	0	0
	0	5	0	0	1	0	2	2	0	1
	0	6	0	0	0	0	4	3	0	0
	0	2	0	0	0	0	0	0	0	0
G3	0	0	3	0	0	0	2	0	0	0
	0	3	0	0	0	0	3	0	0	0
	0	0	0	0	0	0	3	0	0	1
	0	0	0	0	0	0	6	0	0	1
	0	0	0	0	0	0	2	0	0	0
	0	1	0	0	0	0	1	0	0	0
	0	6	0	0	0	0	2	0	0	4
	0	1	0	0	0	0	0	0	0	7
	0	2	0	0	0	0	0	0	0	3
	0	0	0	0	1	1	0	0	0	2
	0	2	0	0	2	0	6	1	0	8
	0	2	0	0	0	0	2	3	0	3
H1	28	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0	0
	19	0	0	0	0	0	0	0	0	0
	19	0	0	0	0	0	0	0	0	0
	52	0	0	0	0	0	0	0	0	0
	28	0	0	0	0	0	0	0	0	0
	37	0	0	0	0	0	0	0	0	0
	38	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0
H2	19	0	0	0	0	0	0	0	0	0
	24	0	0	0	0	0	0	0	0	0
	19	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0
	25	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0
	26	0	0	0	0	0	0	0	0	0
	21	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	29	0	0	0	0	0	0	0	0	0
H3	15	0	0	0	0	0	0	0	0	0
	26	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	25	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0
	18	0	0	0	0	0	0	0	0	0
	16	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0

Appendix 6 continued

	Potentilla erecta	*Poa*	*Carex spicata*	*Lotus*	*Sphagnum*	*Deschampsia*	*Cladonia*	*Betula*	*Lolium*	*E.cinerea*
G1	0	0	0	0	0	0	0	0	0	0
	3	9	8	11	0	0	0	0	0	0
	1	1	0	9	0	0	0	0	0	0
	1	6	0	4	0	0	0	0	0	0
	0	6	0	0	0	0	0	0	0	0
	2	7	0	3	0	0	0	0	0	0
	5	8	0	0	0	0	0	0	0	0
	4	8	0	1	0	0	0	0	0	0
	4	12	0	2	0	0	0	0	0	0
	5	16	0	4	0	0	0	0	0	0
	4	12	0	4	0	0	0	0	0	0
	4	14	0	1	0	0	0	0	0	0
G2	3	0	0	26	0	0	0	0	0	0
	9	0	0	24	0	0	0	0	0	0
	6	0	0	22	0	0	0	0	0	0
	10	0	0	21	0	0	0	0	0	0
	7	5	0	15	0	0	0	0	0	0
	6	5	0	17	0	0	0	0	0	0
	3	12	0	14	0	0	0	0	0	0
	5	16	0	9	0	0	0	0	0	0
	3	13	0	8	0	0	0	0	0	0
	4	14	0	6	0	0	0	0	0	0
	2	17	0	6	0	0	0	0	0	0
	2	20	0	16	0	0	0	0	0	0
G3	0	15	0	0	0	2	0	0	0	0
	0	5	0	0	0	1	0	0	0	0
	0	0	0	0	0	3	0	0	0	0
	0	3	0	0	2	0	0	0	0	0
	0	3	0	0	0	3	0	0	0	0
	0	4	0	0	0	2	0	0	0	0
	2	5	0	12	0	0	0	0	0	0
	3	7	0	12	0	0	0	0	0	0
	2	13	0	2	0	0	0	0	0	0
	10	10	0	20	0	5	0	0	0	0
	6	17	0	2	0	1	0	0	0	0
	1	17	0	0	0	7	0	0	0	0
H1	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	15
	0	0	0	0	0	0	0	0	0	7
	0	0	0	0	0	0	0	0	0	1
	0	0	0	0	0	0	0	0	0	17
	0	0	0	0	0	0	0	0	0	11
	0	0	0	0	0	0	0	0	0	2
	0	0	0	0	0	0	0	0	0	3
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	4
	0	5	0	0	0	0	4	0	0	1
	0	1	0	0	0	0	0	0	1	4
H2	0	6	0	0	0	0	1	0	0	0
	0	0	0	0	0	0	3	0	0	0
	0	2	0	0	0	0	3	0	0	0
	0	3	0	0	0	0	1	0	0	0
	0	1	0	0	0	0	0	0	0	0
	0	8	0	0	0	0	0	0	1	0
	0	4	0	0	0	0	0	0	0	0
	0	3	0	0	0	0	5	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	3	0	0	0
	0	2	0	0	0	0	8	0	0	0
	0	1	0	0	0	0	1	0	0	0
H3	0	1	0	0	0	1	1	0	0	0
	0	2	0	0	2	0	1	0	0	0
	0	0	0	0	0	0	9	0	0	0
	0	1	0	0	1	0	14	0	0	0
	0	0	0	0	3	0	5	0	0	0
	0	0	0	0	0	0	2	0	1	0
	0	0	0	0	1	0	4	0	0	0
	0	0	0	0	0	0	2	0	0	0
	0	1	0	0	0	0	4	0	0	0
	0	1	0	0	0	0	7	0	0	0
	0	0	0	0	0	0	3	0	0	0
	0	2	0	0	4	0	2	0	1	0

Appendix 6 continued

	Myrica	*Eriophorum*	*Narthecium*	*Pinguicula*	*Drosera*	*Pinus*	*Hedera*	*Salix*	*Erodium*
G1	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
G2	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
G3	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
H1	3	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
H2	8	13	0	0	0	0	0	0	0
	23	6	0	0	0	0	0	0	0
	16	8	0	0	0	0	0	0	0
	8	15	0	0	0	0	0	0	0
	17	0	0	0	0	0	0	0	0
	14	6	0	0	0	0	0	0	0
	6	17	0	0	0	0	0	0	0
	4	18	0	0	0	0	0	0	0
	18	11	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	1	0	0	0	0	0	0	0
H3	0	0	0	0	0	0	0	0	0
	10	1	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	3	1	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	16	0	0	0	0	0	0	0	0
	2	3	0	0	0	0	0	0	0
	6	3	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0

Appendix 6 continued

		Agrostis	*Rubus*	*Juncus*	*Carex*	*Festuca*	*Ulex*	*Molinia*	*E.tetralix*	*Luzula*	*Pteridium*
M1	C	2	0	3	1	0	0	64	14	1	1
	C	0	0	0	8	0	0	60	15	0	0
	C	17	0	0	3	0	0	50	7	0	0
	C	5	0	0	0	14	0	26	7	0	0
	C	13	0	0	4	21	0	6	4	0	0
	C	3	0	2	8	7	0	29	10	1	0
	T	0	0	1	0	0	0	67	3	0	0
	T	2	0	1	5	4	0	7	4	0	0
	T	2	0	0	5	13	0	16	6	0	0
	T	4	0	0	6	12	0	13	5	0	0
	T	2	0	4	19	7	0	23	2	0	0
	T	0	0	9	9	1	0	23	8	1	0
M2	C	0	0	0	28	0	0	17	6	0	0
	C	0	0	1	4	0	0	36	10	0	0
	C	6	0	0	15	3	0	21	16	0	0
	C	7	0	8	7	4	0	18	3	0	0
	C	9	0	9	2	3	0	20	17	0	0
	C	10	0	18	0	12	0	20	4	0	0
	T	5	0	1	2	9	0	28	5	0	0
	T	11	0	1	1	5	0	18	8	0	0
	T	21	0	0	3	3	0	27	5	0	0
	T	11	0	4	9	3	0	19	14	0	0
	T	20	0	0	8	6	0	29	5	0	0
	T	10	0	1	3	9	0	19	8	0	0
M3	C	8	0	4	7	11	0	29	0	0	0
	C	9	0	4	7	14	0	27	4	0	0
	C	9	0	3	3	17	0	34	2	0	0
	C	8	0	2	4	11	0	18	0	0	0
	C	5	0	1	9	11	0	30	0	0	0
	C	8	0	0	3	23	0	18	1	0	0
	T	11	0	0	6	5	0	28	1	1	0
	T	11	0	2	4	9	0	21	0	3	0
	T	15	0	2	3	3	0	20	3	0	0
	T	6	0	3	2	2	0	27	2	0	0
	T	7	0	0	2	10	0	21	0	2	0
	T	7	0	3	2	5	0	17	5	5	0
W1	C	7	7	0	0	0	0	0	0	0	49
	C	58	8	0	0	0	0	0	0	0	12
	C	71	3	0	0	0	0	0	0	0	3
	C	66	10	0	0	0	0	0	0	0	10
	C	50	6	0	0	0	0	0	0	0	13
	C	39	5	0	0	0	0	0	0	0	23
	T	2	12	0	1	0	0	0	0	0	25
	T	0	3	0	1	0	0	0	0	0	1
	T	3	29	0	0	0	0	0	0	0	12
	T	0	12	0	0	0	0	0	0	0	18
	T	0	7	0	0	0	0	0	0	0	18
	T	0	22	0	0	0	0	0	0	0	23
W2	C	14	5	0	0	14	0	8	0	0	6
	C	10	8	5	0	10	0	12	0	0	12
	C	7	4	0	0	9	0	9	0	0	8
	C	10	6	1	7	1	0	9	0	0	6
	C	7	10	0	0	12	0	14	0	0	5
	C	7	1	6	5	7	0	14	0	0	6
	T	6	0	4	6	11	0	5	0	0	8
	T	7	10	0	1	8	0	10	0	0	6
	T	17	7	0	0	14	0	11	0	0	6
	T	10	6	4	0	10	0	9	0	0	4
	T	19	3	1	4	6	0	12	0	0	1
	T	7	16	1	0	9	0	16	0	0	1
W3	C	12	8	1	0	4	0	6	0	0	8
	C	13	6	4	4	3	0	10	0	0	8
	C	11	6	2	0	13	0	14	0	0	8
	C	9	10	0	3	3	0	1	0	0	4
	C	10	12	0	0	12	0	9	0	0	4
	C	10	0	5	2	11	0	9	0	0	2
	T	11	4	10	3	8	0	5	0	0	5
	T	11	5	0	0	12	0	12	0	0	5
	T	13	4	0	0	7	0	8	0	0	1
	T	8	5	3	6	8	0	3	0	0	2
	T	17	3	0	1	6	0	9	0	0	1
	T	6	11	1	0	3	0	16	0	0	5

Appendix 6 continued

	Calluna	*Plantago*	*Holcus*	*Geranium*	*Potentilla reptans*	*Ranunculus repens*	*Ranunculus acris*	*Trifolium*	*Salix*	*Centurea*
M1	10	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	18	0	0	0	0	0	0	0	0	0
	18	0	0	0	0	0	0	0	0	0
	29	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0
	44	0	0	0	0	0	0	0	0	0
	27	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0
	18	0	0	0	0	0	0	0	0	0
	28	0	0	0	0	0	0	0	0	0
M2	44	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0	0
M3	15	0	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0
W1	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
W2	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
W3	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0

Appendix 6 continued

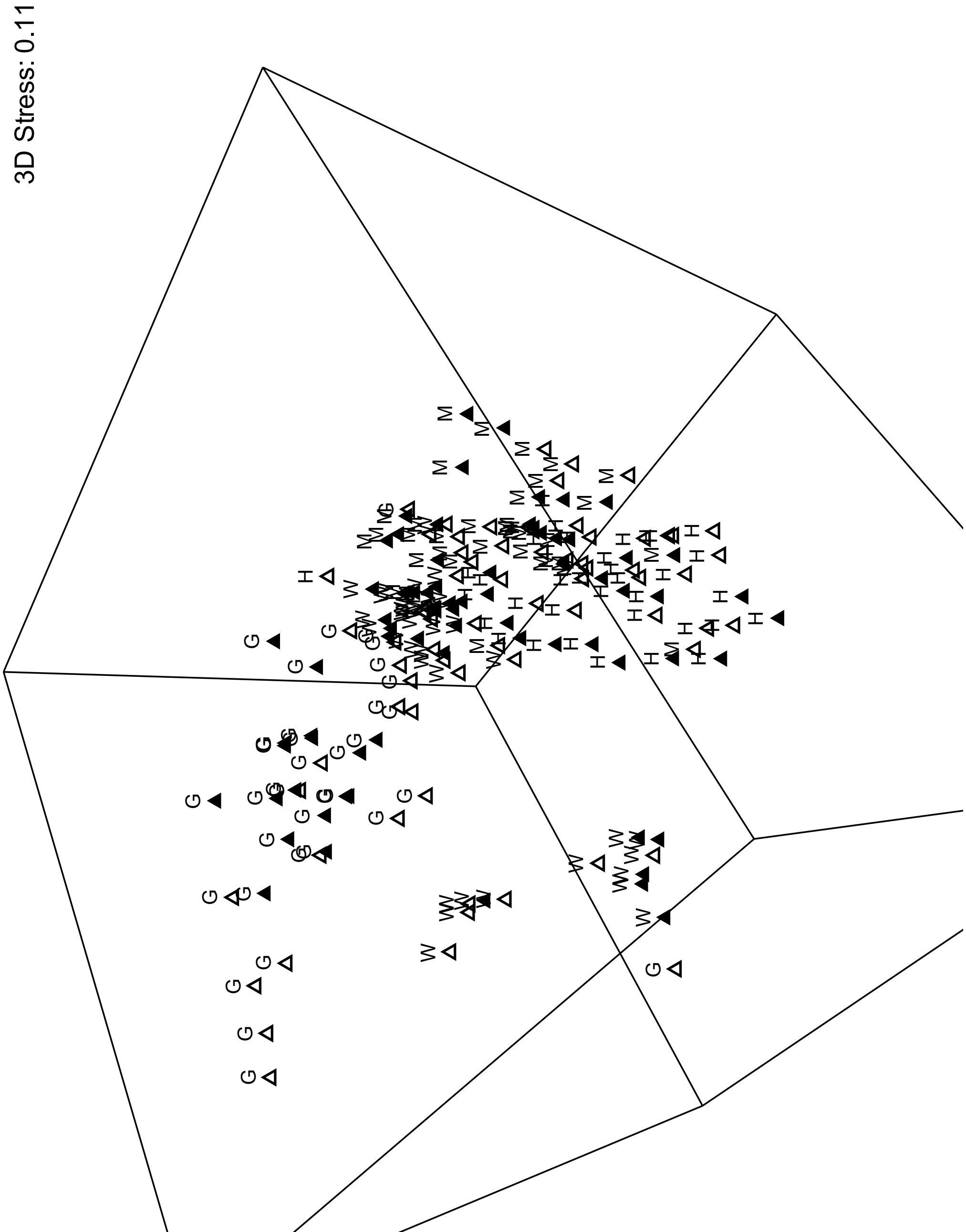
	Potentilla erecta	***Poa***	***Carex spicata***	***Lotus***	***Sphagnum***	***Deschampsia***	***Cladonia***	***Betula***	***Lolium***	***E.cinerea***
M1	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	1	0	0	0	0	0	0	0	0
	0	5	0	0	0	0	4	0	0	0
	0	2	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	2	0	0	0	0	0	0	0	0
	0	1	0	0	0	0	1	0	0	0
	0	6	0	0	0	0	3	0	0	0
	0	4	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
M2	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	2	0	0	2	1	0	0	0	0
	0	3	0	0	2	0	0	0	1	0
	0	0	0	0	3	0	0	0	1	0
	0	0	0	0	4	1	0	0	0	0
	0	0	0	0	2	1	0	0	0	0
	0	0	0	0	14	7	0	0	2	0
	0	13	0	0	3	0	0	0	3	0
	0	0	0	0	4	1	0	0	0	0
	0	10	0	0	3	0	0	0	2	0
	0	1	0	0	3	1	0	0	0	0
M3	0	10	0	0	0	0	0	0	1	0
	0	10	0	0	3	0	0	0	0	0
	0	11	0	0	0	0	0	0	2	0
	0	11	0	0	0	0	0	0	1	0
	0	4	0	0	0	0	0	0	1	0
	0	13	0	0	0	0	0	0	0	0
	0	16	0	0	0	0	0	0	2	0
	0	12	0	0	0	0	2	0	0	0
	0	11	0	0	4	1	0	0	4	0
	0	14	0	0	2	1	2	0	1	0
	0	13	0	0	2	3	0	0	2	0
	0	12	0	0	0	1	1	0	1	0
W1	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	1	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0
W2	0	13	0	0	0	0	0	1	2	0
	0	8	0	0	0	0	0	3	3	0
	0	15	0	0	0	0	0	1	2	0
	0	18	0	0	0	0	0	0	2	0
	0	17	0	0	0	0	0	0	2	0
	0	16	0	0	0	0	0	0	2	0
	0	12	0	0	0	0	0	0	1	0
	0	12	0	0	0	0	0	3	3	0
	0	10	0	0	0	0	0	2	1	0
	0	10	0	0	0	0	0	0	2	0
	0	13	0	0	0	0	0	0	3	0
	0	10	0	0	0	0	0	3	6	0
W3	0	17	0	0	0	0	0	1	2	0
	0	4	0	0	0	0	0	3	1	0
	0	19	0	0	0	0	0	0	3	0
	0	15	0	0	0	0	0	1	3	0
	0	19	0	0	0	0	0	2	4	0
	0	15	0	0	0	0	0	1	1	0
	0	17	0	0	1	1	0	1	0	0
	0	20	0	0	0	1	0	4	2	0
	0	18	0	0	0	0	0	2	3	0
	0	12	0	0	0	0	0	0	3	0
	0	14	0	0	0	1	0	3	4	0
	0	6	0	0	0	0	0	3	5	0

Appendix 6 continued

	Myrica	*Eriophorum*	*Narthecium*	*Pinguicula*	*Drosera*	*Pinus*	*Hedera*	*Salix*	*Erodium*
M1	0	0	2	0	0	0	0	0	0
	0	0	3	0	0	0	0	0	0
	0	0	3	0	0	0	0	0	0
	15	0	9	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0
	7	0	6	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0
	29	0	2	0	0	0	0	0	0
	28	0	1	0	0	0	0	0	0
	28	0	0	0	0	0	0	0	0
	19	0	2	0	0	0	0	0	0
	10	0	9	0	0	0	0	0	0
M2	0	0	0	0	0	0	0	0	0
	41	0	0	0	0	0	0	0	0
	9	0	2	0	0	0	0	0	0
	19	1	0	0	0	0	0	0	0
	17	10	0	0	0	0	0	0	0
	6	0	1	0	0	0	0	0	0
	15	0	1	0	0	0	0	0	0
	9	6	0	0	0	0	0	0	0
	5	3	1	0	0	0	0	0	0
	8	11	2	0	0	0	0	0	0
	0	1	0	0	0	0	0	0	0
	6	0	1	0	0	0	0	0	0
M3	6	1	0	0	0	0	0	0	0
	10	1	0	0	0	0	0	0	0
	12	3	0	0	0	0	0	0	0
	24	4	0	0	0	0	0	0	0
	20	4	0	0	0	0	0	0	0
	13	0	1	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0
	11	7	0	0	0	0	0	0	0
	7	5	0	0	4	0	0	0	0
	1	5	4	0	0	0	0	0	0
	12	0	1	0	3	0	0	0	0
	14	5	0	0	0	0	0	0	0
W1	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	1
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	2	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	3	0
W2	0	0	0	0	0	0	5	0	0
	0	0	0	0	0	0	3	0	0
	0	0	0	0	0	0	5	0	0
	0	0	0	0	0	0	6	0	0
	0	0	0	0	0	0	5	0	0
	0	0	0	0	0	0	5	0	0
	0	0	0	0	0	0	4	0	0
	0	0	0	0	0	0	2	0	0
	0	0	0	0	0	0	0	4	0
	0	0	0	0	0	0	5	1	0
	0	0	0	0	0	0	2	0	0
	0	0	0	0	0	0	4	0	0
W3	0	0	0	0	0	0	14	0	0
	0	0	0	0	0	0	5	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	5	0	0
	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	6	0	0
	0	0	0	0	0	3	0	0	0
	0	0	0	0	0	1	2	0	0
	0	0	0	0	0	2	0	4	0
	0	0	0	0	0	0	11	1	0
	0	0	0	0	0	0	1	0	0
	0	0	0	0	0	0	1	0	0

Appendix 7

Three-dimensional ordination plot for non-metric multidimensional scaling of herbage removal species composition plots, classified for habitat assemblages. (▲treatment plots, Δ control plots; G=Grassland, H=Heath, M=Mire, W=Woodland).



Appendix 8

Foliage height diversity (FHD) indices for each habitat-treatment combination

	Control			Treatment		
	<20	21-60	>60	<20	21-60	>60
G1	44	42	14	96	4	0
	38	53	9	100	0	0
	34	66	0	100	0	0
	56	44	0	100	0	0
	53	40	7	100	0	0
	36	59	5	100	0	0
G2	89	11	0	100	0	0
	92	8	0	100	0	0
	85	15	0	100	0	0
	91	9	0	100	0	0
	84	16	0	100	0	0
	91	9	0	100	0	0
G3	92	8	0	100	0	0
	94	6	0	100	0	0
	87	13	0	100	0	0
	83	17	0	100	0	0
	81	19	0	100	0	0
	91	9	0	100	0	0
TOTAL	1321	444	35	1796	4	0
TOTAL Proportion	0.734	0.247	0.019	0.998	0.002	0.000
p*logp	-0.227	-0.345	-0.077	-0.002	-0.014	-
FHD		**0.6489**			**0.0158**	
H1	85	15	0	87	13	0
	87	13	0	96	4	0
	93	7	0	92	8	0
	92	8	0	97	3	0
	88	12	0	89	11	0
	95	5	0	94	6	0
H2	97	3	0	99	1	0
	98	2	0	98	2	0
	99	1	0	97	3	0
	98	2	0	0	94	6
	97	3	0	97	3	0
	98	2	0	93	7	0
H3	82	18	0	92	8	0
	66	34	0	79	21	0
	89	11	0	93	7	0
	79	21	0	94	6	0
	90	10	0	95	5	0
	85	15	0	80	20	0
TOTAL	1618	182	0	1572	222	6
TOTAL Proportion	0.899	0.101	0.000	0.873	0.123	0.003
p*logp	-0.096	-0.232	-	-0.118	-0.258	-0.019
FHD		**0.3275**			**0.3954**	

	Control			Treatment		
	<20	21-60	>60	<20	21-60	>60
M1	41	38	21	55	32	13
	34	58	8	80	15	5
	38	48	14	81	11	8
	64	24	12	75	24	1
	62	30	8	74	26	0
	67	15	18	70	30	0
M2	98	2	0	66	34	0
	47	51	2	76	24	0
	74	26	0	84	16	0
	64	34	2	80	20	0
	88	12	0	85	15	0
	81	19	0	86	14	0
M3	67	33	0	88	12	0
	70	30	0	82	18	0
	66	28	6	81	19	0
	55	38	7	79	21	0
	64	34	2	84	16	0
	54	43	3	84	16	0
TOTAL	1134	563	103	1410	363	27
TOTAL Proportion	0.630	0.313	0.057	0.783	0.202	0.015
p*logp	-0.291	-0.364	-0.164	-0.191	-0.323	-0.063
FHD		**0.8183**			**0.5772**	
W1	27	73	0	36	64	0
	73	27	0	100	0	0
	17	83	0	91	9	0
	55	44	1	89	11	0
	32	54	14	17	83	0
	41	59	0	34	64	2
W2	79	21	0	74	26	0
	77	23	0	77	23	0
	77	23	0	72	28	0
	73	27	0	72	28	0
	75	25	0	68	32	
	78	22	0	67	33	0
W3	79	21	0	81	19	0
	81	19	0	82	18	0
	85	15	0	87	13	0
	75	25	0	92	8	0
	76	24	0	92	8	0
	78	22	0	90	10	0
TOTAL	1178	607	15	1321	477	2
TOTAL Proportion	0.654	0.337	0.008	0.734	0.265	0.001
p*logp	-0.277	-0.367	-0.040	-0.227	-0.352	-0.008
FHD		**0.6839**			**0.5865**	

Appendix 9

Natural trampling intensities for four transient trampled areas for each habitat type.

Grassland (Opposite Foden)

2011			2010			2009		
	Horse	Cattle		Horse	Cattle		Horse	Cattle
17-Mar	1		15-Apr	6	7	30-Mar	6	8
19-Mar	2		16-Apr	1	3	31-Mar	4	9
20-Mar	5		17-Apr	1		01-Apr	1	
21-Mar		7	18-Apr	3		02-Apr		
22-Mar	1		19-Apr		6	03-Apr		
24-Mar		6	20-Apr			04-Apr	11	
25-Mar	3		21-Apr			05-Apr	7	
26-Mar	1		22-Apr	6	8	06-Apr		
27-Mar	1	6	23-Apr	3	5	07-Apr		
29-Mar	8	5	27-Apr	7	6	08-Apr	2	
30-Mar	6		28-Apr	4	9	09-Apr		
31-Mar	4		29-Apr	8	5	10-Apr		
01-Apr	3		30-Apr	4	7	11-Apr	2	
02-Apr		1	01-May		7	12-Apr	5	
03-Apr	3		02-May		7	13-Apr	2	
04-Apr		4	03-May		7	14-Apr	3	
03-Aug	11		04-May	7		15-Apr	9	
04-Aug	18		05-May	3		16-Apr		
05-Aug	8	4	06-May	8		17-Apr		
06-Aug	12		07-May	2	5	18-Apr		
07-Aug	19		08-May	8	4	19-Apr	3	
08-Aug	16		09-May	2	3	20-Apr	3	
09-Aug	9		10-May	5	5	21-Apr	4	8
10-Aug	23		11-May	6	6	22-Apr	6	6
11-Aug	15		12-May	7	5	23-Apr	3	8
12-Aug	12	6	13-May	8		24-Apr	8	4
13-Aug	13		14-May	6		25-Apr	10	6
14-Aug	6		15-May	7		26-Apr	6	
15-Aug	10		16-May	2		27-Apr	5	
16-Aug	14	8	03-Jun	8	6	28-Apr	3	
17-Aug	11	1	04-Jun	7	3	29-Apr	1	
18-Aug	11	3	05-Jun	4		30-Apr	3	
19-Aug	19		06-Jun		7	01-May		
20-Aug	22		07-Jun			02-May		7
21-Aug	10	8	08-Jun		7	03-May		1
22-Aug	6		09-Jun	4	3	04-May	7	7
23-Aug	8	6	10-Jun	2	4	05-May	5	
24-Aug	19	7	11-Jun	3	4	16-May	3	
25-Aug	9		12-Jun	7		17-May	11	
26-Aug	9	7	13-Jun	1		18-May	6	
27-Aug	8		14-Jun	6		19-May	4	
28-Aug	14		15-Jun	5	6	20-May		
29-Aug	3	7	16-Jun	1		21-May	1	
30-Aug	4	7	17-Jun	8		22-May	7	
31-Aug		7	18-Jun	4		23-May	9	5
01-Sep	6	7	19-Jun	1		24-May	7	
02-Sep	6		20-Jun	4		25-May	5	
03-Sep	10		21-Jun	3		26-May	5	
04-Sep	15	8	22-Jun	4	4	27-May	10	
05-Sep	11	4	23-Jun	7	9	28-May	8	
06-Sep	15		25-Jun	5	4	29-May	1	
07-Sep	12		26-Jun	5	4	20-Jun		
08-Sep	12		27-Jun	8	4	21-Jun	4	8
09-Sep	4		28-Jun		5	22-Jun	8	6
10-Sep	9	5	29-Jun		8	23-Jun	1	7
11-Sep	23		30-Jun			24-Jun	6	8
12-Sep	14		01-Jul			25-Jun	11	
13-Sep	11		02-Jul	8		26-Jun	5	
16-Sep	6	3	03-Jul	1		27-Jun		
17-Sep		10	04-Jul	2	4	28-Jun		
18-Sep	1		05-Jul	1	7	29-Jun		
19-Sep	2	13	06-Jul		3	30-Jun		5
20-Sep	10		07-Jul		3	01-Jul	9	
21-Sep	5		08-Jul		6	02-Jul	5	
22-Sep	6		09-Jul		8	03-Jul	11	4
23-Sep	3		10-Jul		4	04-Jul	9	5
24-Sep	4		11-Jul		9	05-Jul	6	
25-Sep	2		12-Jul	1	3	06-Jul	6	
26-Sep	2		13-Jul	8	4	07-Jul	3	
27-Sep	2		14-Jul	2	8	08-Jul	8	9
			15-Jul		9	09-Jul		9
			16-Jul	4	9	10-Jul		
			17-Jul	3	3	11-Jul		

Appendix 9 continued

			18-Jul	3	4	12-Jul	10	
			19-Jul	4	9	13-Jul	20	
			20-Jul	6	4	14-Jul	1	
			21-Jul		3	15-Jul	2	
			22-Jul	7		16-Jul		8
			23-Jul	5		17-Jul	9	5
			24-Jul	5		18-Jul	7	6
			25-Jul	4		19-Jul	1	10
			26-Jul	3		20-Jul	2	6
			27-Jul	3		21-Jul	4	7
			28-Jul	6	6	22-Jul	4	4
			29-Jul		7	23-Jul	7	
			30-Jul	4		24-Jul	10	
			31-Jul	2		25-Jul	2	
			01-Aug	5		26-Jul	5	
			02-Aug	3	6	27-Jul	3	6
			03-Aug	5	7	28-Jul	3	9
			04-Aug	1	5	29-Jul	7	5
			05-Aug	2		30-Jul		
			06-Aug	8	5	31-Jul		
			07-Aug	7	4	01-Aug	9	7
			08-Aug	2	8	02-Aug	4	9
			09-Aug		7	03-Aug	11	5
			10-Aug		9	04-Aug	6	3
			11-Aug		5	05-Aug	7	4
			12-Aug		4	06-Aug	16	8
			13-Aug		8	07-Aug	10	
			14-Aug	3	7	08-Aug	11	
			15-Aug	2	9	09-Aug	8	
			16-Aug	1	5	10-Aug	3	
			17-Aug	3		11-Aug	2	
			18-Aug	1		12-Aug	8	
			19-Aug	5	1	13-Aug	1	
			20-Aug	8	1	14-Aug	11	6
			21-Aug	6	1	15-Aug	7	3
			22-Aug			16-Aug	10	
			23-Aug		9	17-Aug	1	
			24-Aug	3		18-Aug	18	
			25-Aug	9	7	19-Aug	8	
			26-Aug		6	20-Aug	2	
			27-Aug	6	5	21-Aug	8	
			28-Aug		8	22-Aug	10	3
			29-Aug			23-Aug	2	
			30-Aug	7		24-Aug	8	3
			31-Aug	8		25-Aug	13	
			01-Sep	1		26-Aug	10	7
			02-Sep		7	27-Aug	7	
			03-Sep		4	28-Aug	11	9
			04-Sep		3	29-Aug		6
			05-Sep	6		30-Aug		
			06-Sep	10		31-Aug		
			07-Sep	10	2	01-Sep	4	5
			08-Sep	5	3	02-Sep	8	3
			09-Sep	7	1	03-Sep	11	2
			10-Sep	11	5	04-Sep	10	1
			11-Sep	5	4	05-Sep	7	
			12-Sep	2				
			13-Sep	2				
			14-Sep	10				
			15-Sep	3				
			16-Sep	3	7			
			17-Sep	12	7			
			18-Sep					
			19-Sep					
			20-Sep					
			21-Sep					
			22-Sep	3				
			23-Sep	1	4			
			24-Sep	8				
			25-Sep	5				
			26-Sep	11	8			
			27-Sep	4				
			28-Sep	3				
			29-Sep	12	7			
			30-Sep	3	6			
total events	568	150		525	491		647	280
no of days	64	25		109	89		102	47
prop	8.875	6.000		4.81651	5.51685		6.343137	5.957447

Appendix 9 continued

Heath (Vixen track)								
2011			2010			2009		
	Horse	Cattle		Horse	Cattle		Horse	Cattle
21-Jul	5	8	16-Mar	9	2	03-Mar	3	3
22-Jul	3		17-Mar		5	05-Mar	1	7
23-Jul			18-Mar	11		06-Mar		6
24-Jul	3		19-Mar	5	5	11-Mar	3	3
25-Jul	3		20-Mar	8		14-Mar		7
26-Jul	3		21-Mar	8	9	15-Mar		1
27-Jul	2		22-Mar		4	16-Mar		10
28-Jul	3		23-Mar		6	25-Mar		11
29-Jul	3		24-Mar		7	03-Apr		1
30-Jul	8		25-Mar	3		04-Apr	3	1
31-Jul	11		26-Mar	11	2	13-Apr		4
01-Aug	3	14	27-Mar	9	3	20-Apr		3
02-Aug			28-Mar	1	6	23-Apr		3
03-Aug	3		29-Mar	1		01-May	2	0
04-Aug	3	8	30-Mar	5	3	04-May	2	
05-Aug			31-Mar	5	4	05-May	1	
06-Aug			01-Apr	2		06-May	1	9
07-Aug			02-Apr	8	5	07-May	2	
08-Aug			03-Apr	2	8	10-May		1
09-Aug	5		04-Apr		5	14-May		10
10-Aug			05-Apr	2	4	15-May	0	14
11-Aug	2	7	06-Apr	4	8	16-May	9	15
12-Aug			07-Apr	10		16-May		
13-Aug			08-Apr	1	7	17-May		
14-Aug	9	4	09-Apr		3	18-May	5	3
15-Aug			10-Apr	2	3	19-May	7	1
16-Aug			11-Apr	9	8	20-May	7	1
17-Aug	5		12-Apr	1	7	21-May	2	6
18-Aug			17-Apr	10	3	22-May		
19-Aug			18-Apr	6	5	23-May		2
20-Aug	1	4	19-Apr	9	6	24-May		2
21-Aug	3		20-Apr	5	4	01-Jul	8	1
22-Aug	3		21-Apr	2		02-Jul		
23-Aug	3		22-Apr	6	6	03-Jul	7	2
24-Aug			23-Apr			04-Jul		6
25-Aug			24-Apr		2	05-Jul	6	7
26-Aug	1		25-Apr		7	06-Jul		6
27-Aug	4	7	03-Jun		2	07-Jul		
28-Aug	2		04-Jun	11	5	08-Jul		3
29-Aug	3		05-Jun	10	7	09-Jul	7	4
30-Aug	3		06-Jun		7	10-Jul	9	7
31-Aug	7		07-Jun	3	7	11-Jul	8	4
01-Sep			08-Jun	9	2	12-Jul	4	
02-Sep		6	09-Jun	11	10	13-Jul		3
03-Sep			10-Jun	3		14-Jul		
04-Sep	3		11-Jun	3		15-Jul	7	5
05-Sep			12-Jun	9	1	16-Jul		5
06-Sep			13-Jun	8	2	17-Jul		
07-Sep			14-Jun	5	1	18-Jul	3	4
08-Sep		7	15-Jun	1		19-Jul	9	2
09-Sep	3	6	16-Jun	3	15	20-Jul	7	
10-Sep			17-Jun	6	2	21-Jul	3	3
11-Sep			18-Jun		2	22-Jul	3	3
12-Sep			19-Jun			23-Jul	2	5
13-Sep			07-Aug			24-Jul	3	4
14-Sep		6	08-Aug	4	1	25-Jul		3
15-Sep	3	2	09-Aug	3	4	26-Jul		6
16-Sep	3		10-Aug	4	4	27-Jul		2
17-Sep			11-Aug	7	4	28-Jul	3	
18-Sep			12-Aug	8	5	29-Jul		4
19-Sep			13-Aug	3	1	30-Jul	3	4
20-Sep			14-Aug	6	6	31-Jul	3	6
21-Sep			15-Aug	5	21	01-Aug	2	
22-Sep			16-Aug	11		02-Aug	8	
			17-Aug	9	1	03-Aug		
			18-Aug	2	6	04-Aug	5	7
			19-Aug	8	18	18-Aug	2	3
			20-Aug			19-Aug	3	4
			21-Aug			20-Aug	7	2
			22-Aug		7	21-Aug	4	6
			23-Aug	5	2	22-Aug		
			24-Aug	6	4	23-Aug		3
			25-Aug	8	9	24-Aug	8	4
			26-Aug	2	1	25-Aug	5	2
			27-Aug	9	2	26-Aug	3	3

Appendix 9 continued

			28-Aug	9	4	27-Aug	8	5
			29-Aug	10	1	28-Aug		
			30-Aug	16		29-Aug		6
			31-Aug	9		30-Aug	4	
			01-Sep	1	6	31-Aug	4	4
			02-Sep	9		01-Sep	9	6
			03-Sep	1	8	02-Sep		6
			04-Sep		4	03-Sep		5
			05-Sep			04-Sep	7	7
			06-Sep		9	05-Sep	8	
			07-Sep	8	6	06-Sep	9	
			08-Sep	2	8	07-Sep	3	6
			09-Sep	7	9	08-Sep	3	3
			10-Sep	6		09-Sep	3	7
			11-Sep	7		10-Sep	6	7
			12-Sep	8	4	11-Sep	9	2
			13-Sep	3	4	12-Sep		
			14-Sep	3	1	13-Sep	2	
			15-Sep	3	9			
			16-Sep	3				
			17-Sep	5	2			
			18-Sep	3	7			
			19-Sep	2				
total events	116	79		452	388		265	321
no of days	31	12		78	74		56	70
prop	3.74194	6.58333		5.79487	5.24324		4.73214	4.58571

Mire (Near Laffan)								
2011			2010			2009		
	Horse	Cattle		Horse	Cattle		Horse	Cattle
11-Mar	2	7	20-Apr	5		05-May	1	8
12-Mar	6	2	21-Apr	3	5	06-May	1	7
13-Mar	6	6	22-Apr		3	07-May	5	
14-Mar	2	5	23-Apr	3	6	08-May		6
15-Mar		7	24-Apr	2	3	09-May	5	
16-Mar	6	7	25-Apr	1		10-May	3	4
17-Mar		3	26-Apr	6		11-May		7
18-Mar	2	6	27-Apr			12-May	2	
19-Mar	5	7	28-Apr			13-May	3	7
20-Mar	6		29-Apr			14-May	4	7
21-Mar	3		30-Apr	2	6	15-May	2	7
22-Mar	1		01-May	4	7	16-May	4	7
23-Mar	6		02-May	2	7	17-May		
24-Mar		4	03-May			18-May	6	6
25-Mar		7	04-May	3		19-May	1	2
26-Mar		4	05-May	1		20-May	5	6
27-Mar		6	06-May	1	7	21-May		5
28-Mar		4	07-May	5	3	22-May	3	2
29-Mar			08-May	4	2	23-May	6	7
30-Mar	2	2	09-May	1	7	24-May	5	
31-Mar	6	7	10-May	5		25-May	6	
01-Apr	5	6	11-May	6	2	26-May		
02-Apr	6	4	12-May		3	27-May		
03-Apr			13-May		4	28-May	2	
04-Apr	3		14-May	3	3	29-May	4	
05-Apr	5	2	15-May			30-May	4	
06-Apr	4	7	16-May		3	31-May	6	4
07-Apr	5	2	17-May		2	01-Jun		6
08-Apr	5	6	18-May	3	3	02-Jun		4
09-Apr	2	4	19-May	5	7	03-Jun		2
10-Apr	5	7	20-May	2	5	04-Jun		4
11-Apr	3	5	21-May	2		05-Jun		2

Appendix 9 continued

12-Apr	6	4	22-May	5		06-Jun	4	
13-Apr	6	6	23-May	6		07-Jun	4	4
14-Apr		5	24-May	5	3	20-Jun	5	7
15-Apr			25-May	5	7	21-Jun	4	7
29-Apr	1	6	26-May	1	3	22-Jun	4	5
30-Apr	6	6	27-May	6	2	23-Jun	4	4
01-May	1		28-May		4	24-Jun		
02-May	1		29-May	3	5	25-Jun	5	4
03-May	6		30-May		5	26-Jun		7
04-May	2	2	31-May	6		27-Jun	4	2
05-May		6	01-Jun	3	2	28-Jun	4	7
06-May		4	02-Jun		7	29-Jun	2	7
07-May		7	03-Jun	2	4	30-Jun		3
08-May		5	04-Jun	5		01-Jul		3
09-May		3	05-Jun	4		02-Jul		5
10-May		5	06-Jun			03-Jul	6	
11-May	1	2	07-Jun	1	6	30-May	6	7
12-May	6	6	08-Jun	4	7	31-May	1	7
13-May	6	3	09-Jun	5	4	01-Jun	3	7
14-May	6		10-Jun	6	4	02-Jun	3	2
15-May	1		11-Jun	4	7	21-Jun	4	3
16-May			12-Jun	1	6	22-Jun	5	4
17-May	6	2	13-Jun		7	23-Jun		6
18-May	6	2	14-Jun		3	24-Jun	4	4
19-May	3	5	15-Jun		5	25-Jun	1	
20-May	4		16-Jun		2	26-Jun		4
21-May		5	17-Jun			27-Jun	2	4
22-May	2	7	18-Jun		5	28-Jun	4	2
01-Jun	6	7	19-Jun		4	29-Jun		5
02-Jun		8	20-Jun	4	7	30-Jun	3	3
03-Jun	1		21-Jun	2	5	08-Aug	3	4
04-Jun	5	1	22-Jun	4		09-Aug	3	3
05-Jun	5		23-Jun	1	5	01-Sep	5	
06-Jun	3	7	24-Jun	1		02-Sep	5	5
07-Jun	3	7	25-Jun			03-Sep	2	3
08-Jun	3	5	26-Jun		7	04-Sep		
09-Jun	3	7	27-Jun	3	5	05-Sep		3
10-Jun			28-Jun		7	06-Sep	3	3
18-Jun		3	29-Jun	3	7	07-Sep		
19-Jun		2	30-Jun	3	7	08-Sep	2	3
20-Jun		2	01-Jul		3	09-Sep	6	4
21-Jun			02-Jul	3		10-Sep	3	3
22-Jun	3	1	03-Jul	3		11-Sep	3	
23-Jun	3		04-Jul	1	4	12-Sep		4
24-Jun	6	7	05-Jul	3	3	13-Sep	3	
25-Jun	3	4	06-Jul	4	4	14-Sep	6	4
26-Jun		3	07-Jul	2	1	15-Sep		
27-Jun			08-Jul			16-Sep	6	
28-Jun		7	09-Jul			17-Sep	3	
29-Jun	3	7	10-Jul		2	18-Sep	5	7
			11-Jul	4	6	19-Sep	6	7
			12-Jul	2	4	20-Sep		5
			13-Jul	3		21-Sep	1	3
			14-Jul	3	5	22-Sep	4	7
			15-Jul	3	5	23-Sep	1	7
			16-Jul	6		24-Sep	2	7
			17-Jul		4	25-Sep		3
			18-Jul	6	3	26-Sep	3	
			19-Jul	4	3	27-Sep	3	7
			20-Jul	2		28-Sep	3	8
			21-Jul	3	7	29-Sep		7
			22-Jul	3	7	08-Sep		7
			23-Jul	3		09-Sep	3	

Appendix 9 continued

			24-Jul		7	10-Sep	4	
			11-Aug		1			
			12-Aug	6				
			13-Aug	3				
			14-Aug	9				
			15-Aug	3				
			16-Aug	3	7			
			17-Aug	3	5			
			18-Aug					
			19-Aug		7			
			20-Aug	3	2			
			21-Aug		2			
			22-Aug	1	2			
total events	213	296		251	334		248	347
no of days	54	61		74	73		68	70
prop	3.9444	4.8525		3.3919	4.5753		3.6471	4.9571

Woodland (Near Laffan)

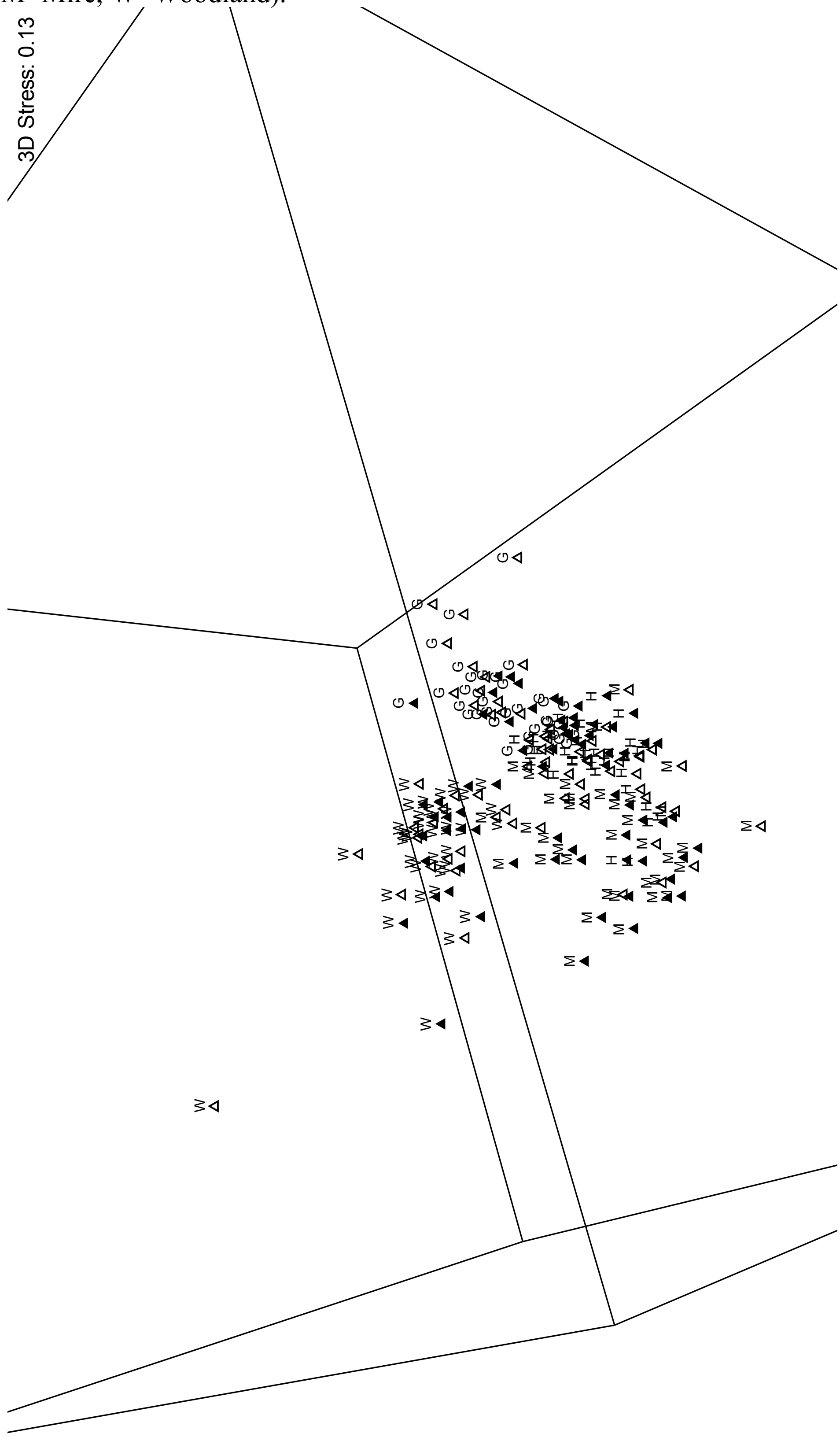
2011			2010			2009		
	Horse	Cattle		Horse	Cattle			
01-May	4	7	07-Apr	5		03-Mar	1	8
02-May	4	2	08-Apr	5	5	04-Mar	1	3
03-May	1		09-Apr	1	3	05-Mar	1	
04-May	1	1	10-Apr	3	6	06-Mar	3	6
05-May			11-Apr	3	3	07-Mar		
06-May			12-Apr			08-Mar		4
07-May	3	3	13-Apr	6		09-Mar		7
08-May		5	14-Apr	4		10-Mar		
09-May		7	15-Apr	4		11-Mar		7
10-May	6	2	16-Apr			12-Mar		
11-May	2	3	17-Apr	5	6	13-Mar	3	3
12-May	6	6	18-Apr	1	7	14-Mar	4	
13-May	3		19-Apr	4	7	15-Mar	2	7
14-May	3		20-Apr	1		16-Mar	6	4
15-May	2		21-Apr	2		17-Mar	4	
16-May			22-Apr	2		18-Mar	4	4
17-May	6	4	23-Apr		7	19-Mar	5	6
18-May	3	6	24-Apr		7	20-Mar	3	4
19-May			06-May		5	21-Mar		2
20-May	2		07-May		4	22-Mar	4	8
21-May	2	1	08-May	3		02-May	3	6
22-May	3	5	09-May		7	03-May	1	4
23-May		6	10-May	3	3	04-May	3	
24-May		3	11-May	1	4	05-May	3	4
25-May			12-May	4		06-May	3	5
02-Jun			13-May	3	7	07-May	6	6
03-Jun		1	14-May	5	7	08-May	5	6
04-Jun		1	15-May		5	09-May	5	
05-Jun		5	16-May	6	4	10-May	3	3
06-Jun		6	03-Jun	4	4	11-May	4	
07-Jun	3	2	04-Jun	2	5	12-May	2	7
08-Jun	3		18-Jul		5	13-May	6	4
09-Jun	4		19-Jul	4	5	14-May	4	6
10-Jun	5		20-Jul	3	4	15-May		3
11-Jun	5	8	21-Jul	3	4	16-May	3	
12-Jun			22-Jul		3	17-May	1	7
13-Jun		4	23-Jul	3	4	18-May	4	4
14-Jun		6	24-Jul	6		19-May		
15-Jun		1	25-Jul	5		20-May	4	
16-Jun	3		26-Jul			21-May	2	7
17-Jun	3	1	27-Jul	1	7	22-May	1	7
18-Jun	2		28-Jul	3	5	23-May	6	
19-Jun	6	2	29-Jul		6	24-May	4	
20-Jun	6	5	30-Jul	5	7	25-May	5	3
21-Jun	3	5	31-Jul	3	7	26-May	5	4

Appendix 9 continued

22-Jun		6	01-Aug	3		27-May	6	6
23-Jun	6	2	02-Aug	3	2	28-May	1	
24-Jun			03-Aug		2	29-May	1	
25-Jun	2	2	04-Aug	5		30-May	2	
26-Jun	2		05-Aug	3		31-May	4	6
27-Jun		5	06-Aug			01-Jun	4	6
28-Jun	6	3	07-Aug	2	3	02-Jun	4	4
29-Jun	3	4	08-Aug	2	5	21-Jun	5	
30-Jun	3	5	09-Aug	5	6	22-Jun	2	3
01-Jul		5	10-Aug		2	23-Jun		4
02-Jul	2		11-Aug	4	3	24-Jun		7
03-Jul		3	12-Aug	5		25-Jun		5
04-Jul	2		13-Aug		5	26-Jun		7
05-Jul	5	5	14-Aug	3	1	27-Jun		7
10-Aug	3	7	15-Aug		2	28-Jun		4
11-Aug	3	7	16-Aug	3		29-Jun	6	3
12-Aug	3	8	17-Aug			30-Jun	4	
13-Aug			18-Aug	2	4	08-Aug	3	6
14-Aug		1	19-Aug	3		09-Aug	1	5
15-Aug			20-Aug	3	6	10-Aug	3	
16-Aug	3	7	21-Aug	6	4	11-Aug	3	5
17-Aug		6	22-Aug	6		12-Aug	3	3
18-Aug		5	23-Aug			13-Aug	3	
19-Aug	2	7	24-Aug	3		14-Aug	3	3
20-Aug	2		25-Aug			15-Aug	3	3
			26-Aug	3	9	16-Aug		
			27-Aug	3	9	17-Aug	2	3
			28-Aug		3	18-Aug	6	4
			29-Aug	3		19-Aug	3	3
			30-Aug	3		20-Aug	3	
			31-Aug	1	4	21-Aug	3	4
			01-Sep	3	3	22-Aug	3	
			02-Sep	4	4	23-Aug	6	4
			03-Sep	2	1	24-Aug	2	
			04-Sep			25-Aug	6	
			05-Sep			26-Aug	3	
			06-Sep		2	27-Aug	5	7
			07-Sep	4	6	28-Aug	6	7
			08-Sep	2	4	29-Aug		5
			09-Sep	3		30-Aug	1	5
			10-Sep	3	5	31-Aug	4	3
			11-Sep	3	5	01-Sep	1	3
			12-Sep	6		02-Sep	2	3
			13-Sep		4	03-Sep		3
			14-Sep	6	3	04-Sep		
			15-Sep	4	3	05-Sep		7
			16-Sep	2		06-Sep		8
			17-Sep	3	3	07-Sep		7
			18-Sep	3		08-Sep	1	7
			19-Sep	3	1	09-Sep	5	
			20-Sep		1	10-Sep	4	
			21-Sep		1	11-Sep	1	
			22-Sep	6		12-Sep	6	7
			23-Sep	3		13-Sep	4	5
			24-Sep	9		14-Sep	1	5
			25-Sep	3		15-Sep	6	6
			26-Sep	3	7	16-Sep	5	4
			27-Sep	3	5	17-Sep		5
			28-Sep		7	18-Sep	3	4
			29-Sep		7	19-Sep	2	1
						20-Sep		6
						21-Sep		7
						22-Sep	7	7
						23-Sep		
						24-Sep	1	7
						25-Sep	11	5
						26-Sep		4
						27-Sep	2	
						28-Sep	8	4
						29-Sep	10	3
total events	141	196		265	305		318	409
no of days	42	46		76	67		88	82
prop	3.35714	4.26087		3.48684	4.55224		3.61364	4.9878

Appendix 10

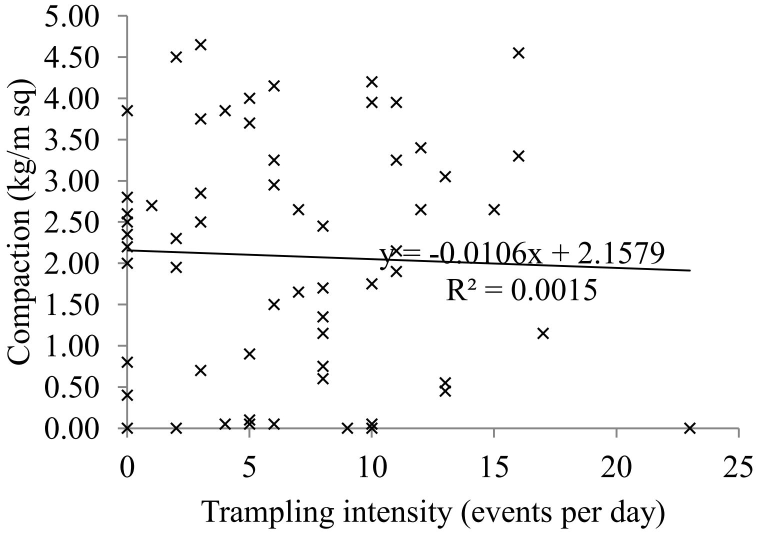
Three-dimensional ordination plot for non-metric multidimensional scaling of trampling species composition plots. (▲treatment plots, Δ control plots; G=Grassland, H=Heath, M=Mire, W=Woodland).



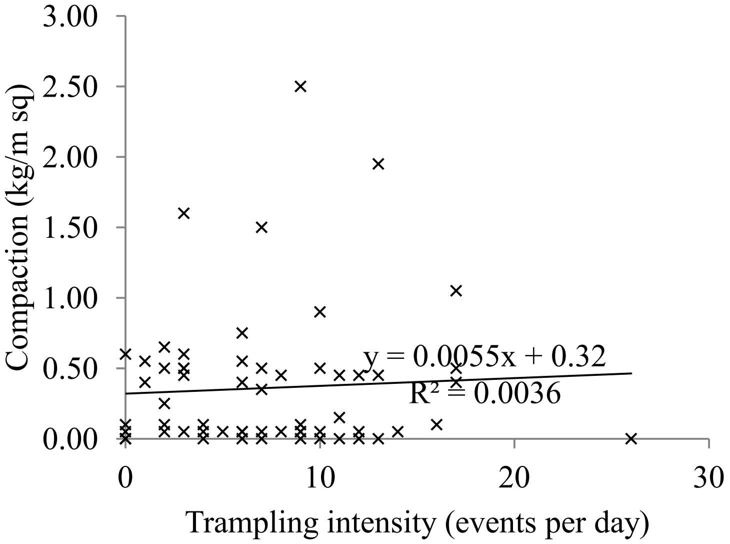
Appendix 11

Regression plots for trampling intensity and soil compaction for each habitat.

(a) Grassland

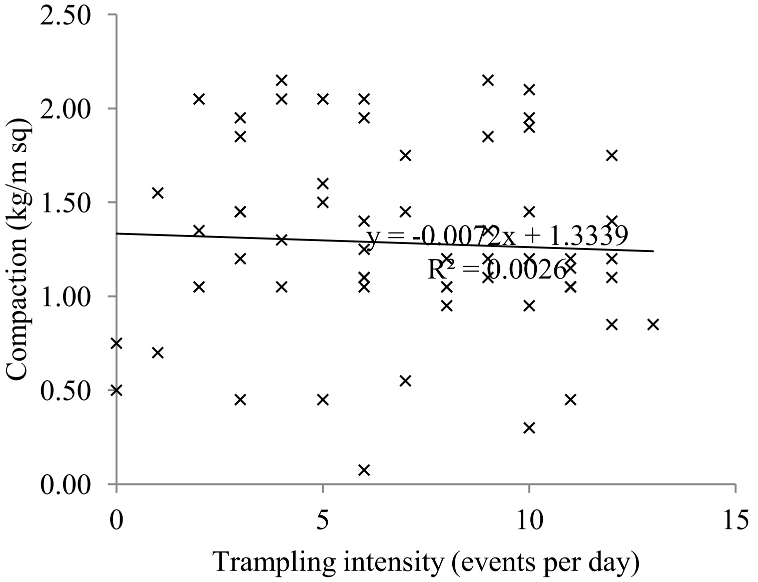


(b) Heath

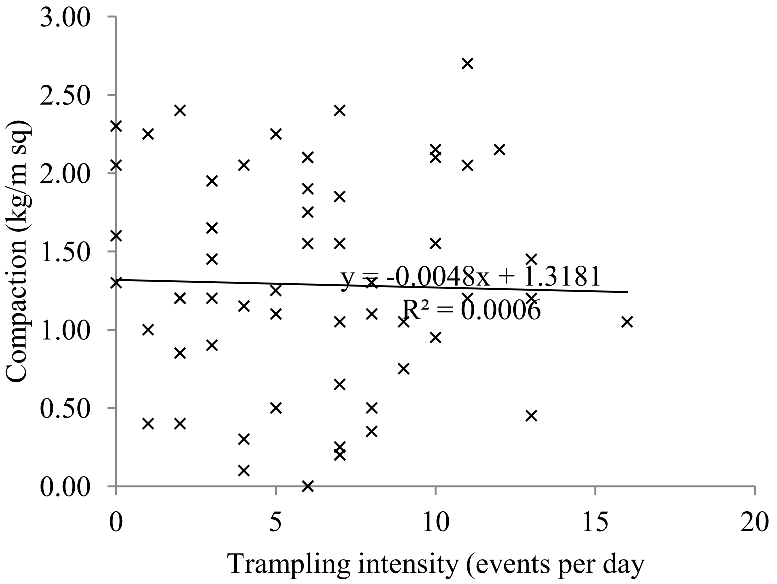


Appendix 11 continued

(c) Mire



(d) Woodland



Appendix 12

Soil chemical compositions from pooled samples for dunging plots across all habitat types. (H=horse, C= cattle, N=non-wormed, W=wormed, T=treatment, C=control)

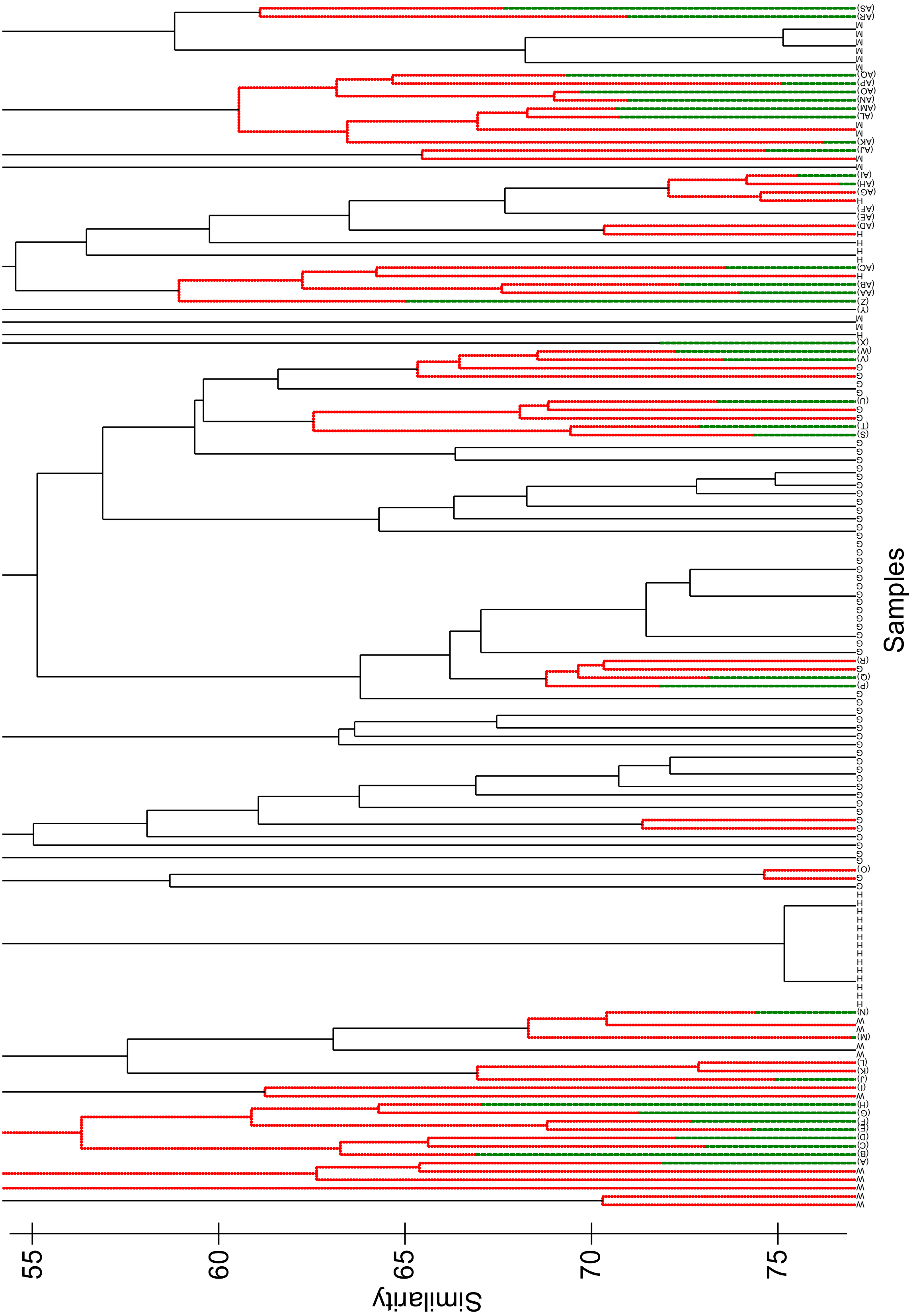
Habitat	Animal	Worming regime	Treatment	pH	P	K	Mg
Grassland	H	N	T	5.9	7.0	48	61
Grassland	H	N	C	5.7	7.0	62	60
Grassland	C	N	T	6.8	6.4	61	75
Grassland	C	N	C	6.3	6.4	43	67
Grassland	H	W	T	5.4	6.6	55	66
Grassland	H	W	C	5.2	6.8	42	68
Grassland	C	W	T	5.9	6.3	48	72
Grassland	C	W	C	6.0	6.3	59	75
Grassland	H	N	T	5.2	6.1	52	44
Grassland	H	N	C	5.0	6.8	48	40
Grassland	C	N	T	5.9	6.5	60	42
Grassland	C	N	C	5.6	6.9	58	49
Grassland	H	W	T	5.6	6.3	48	44
Grassland	H	W	C	5.5	6.3	49	52
Grassland	C	W	T	6.3	6.3	62	69
Grassland	C	W	C	6.2	6.1	58	63
Grassland	H	N	T	5.0	6.2	55	45
Grassland	H	N	C	5.2	7.8	49	36
Grassland	C	N	T	5.8	6.4	37	41
Grassland	C	N	C	5.6	6.8	64	51
Grassland	H	W	T	5.8	6.3	54	47
Grassland	H	W	C	5.5	6.4	50	51
Grassland	C	W	T	6.4	6.0	47	66
Grassland	C	W	C	5.9	6.1	52	62
Heath	H	N	T	4.7	7.6	40	25
Heath	H	N	C	4.5	7.2	57	31
Heath	C	N	T	4.5	7.6	47	20
Heath	C	N	C	4.4	7.4	65	19
Heath	H	W	T	4.4	7.4	51	22
Heath	H	W	C	4.5	7.2	48	28
Heath	C	W	T	4.1	7.7	56	20
Heath	C	W	C	4.1	7.4	52	23
Heath	H	N	T	4.8	5.5	45	30
Heath	H	N	C	4.4	5.2	42	34
Heath	C	N	T	4.7	5.3	48	24
Heath	C	N	C	4.5	5.8	46	29
Heath	H	W	T	4.5	5.7	49	27
Heath	H	W	C	4.3	5.3	46	34
Heath	C	W	T	4.4	5.5	55	26
Heath	C	W	C	4.1	5.3	52	31
Heath	H	N	T	4.2	5.4	44	28
Heath	H	N	C	4.2	5.2	42	35
Heath	C	N	T	4.3	5.2	48	22
Heath	C	N	C	4.1	6.2	47	27
Heath	H	W	T	4.4	5.9	49	29
Heath	H	W	C	4.2	5.4	48	33
Heath	C	W	T	4.3	5.5	54	27
Heath	C	W	C	4.2	5.5	51	30

Appendix 12 continued

Habitat	Animal	Worming regime	Treatment	pH	P	K	Mg
Mire	H	N	T	4.9	5.4	44	43
Mire	H	N	C	4.9	5.8	60	63
Mire	C	N	T	5.5	5.4	31	44
Mire	C	N	C	5.0	4.8	22	29
Mire	H	W	T	5.1	5.5	49	41
Mire	H	W	C	4.7	5.2	52	48
Mire	C	W	T	5.5	5.4	41	45
Mire	C	W	C	5.1	5.1	39	38
Mire	H	N	T	4.7	5.5	33	24
Mire	H	N	C	4.4	5.2	25	20
Mire	C	N	T	4.6	5.3	33	24
Mire	C	N	C	4.3	5.0	45	20
Mire	H	W	T	4.5	4.4	35	26
Mire	H	W	C	4.1	4.1	27	22
Mire	C	W	T	4.5	4.5	33	28
Mire	C	W	C	4.2	4.2	40	23
Mire	H	N	T	4.7	5.4	30	22
Mire	H	N	C	4.6	5.2	24	21
Mire	C	N	T	4.5	5.2	31	24
Mire	C	N	C	4.2	5.0	43	23
Mire	H	W	T	4.4	5.4	33	25
Mire	H	W	C	4.1	5.3	28	23
Mire	C	W	T	4.3	5.4	32	27
Mire	C	W	C	4.1	4.9	41	25
Woodland	H	N	T	4.3	7.8	45	37
Woodland	H	N	C	4.4	8.6	49	35
Woodland	C	N	T	4.3	10.0	136	70
Woodland	C	N	C	4.4	10.0	108	85
Woodland	H	W	T	4.2	7.6	51	35
Woodland	H	W	C	4.4	8.5	53	36
Woodland	C	W	T	4.4	10.7	131	67
Woodland	C	W	C	4.5	10.9	110	74
Woodland	H	N	T	3.5	5.3	98	16
Woodland	H	N	C	3.7	6.2	54	15
Woodland	C	N	T	3.5	8.5	101	35
Woodland	C	N	C	3.9	9.4	73	40
Woodland	H	W	T	3.5	5.2	79	21
Woodland	H	W	C	3.9	5.9	65	25
Woodland	C	W	T	3.4	9.5	95	39
Woodland	C	W	C	3.8	9.9	79	45
Woodland	H	N	T	3.6	5.4	100	15
Woodland	H	N	C	3.7	6.0	48	13
Woodland	C	N	T	3.6	9.0	104	33
Woodland	C	N	C	3.8	9.8	79	42
Woodland	H	W	T	3.6	5.3	77	19
Woodland	H	W	C	3.8	6.1	69	24
Woodland	C	W	T	3.6	9.7	101	35
Woodland	C	W	C	3.9	10.2	82	44

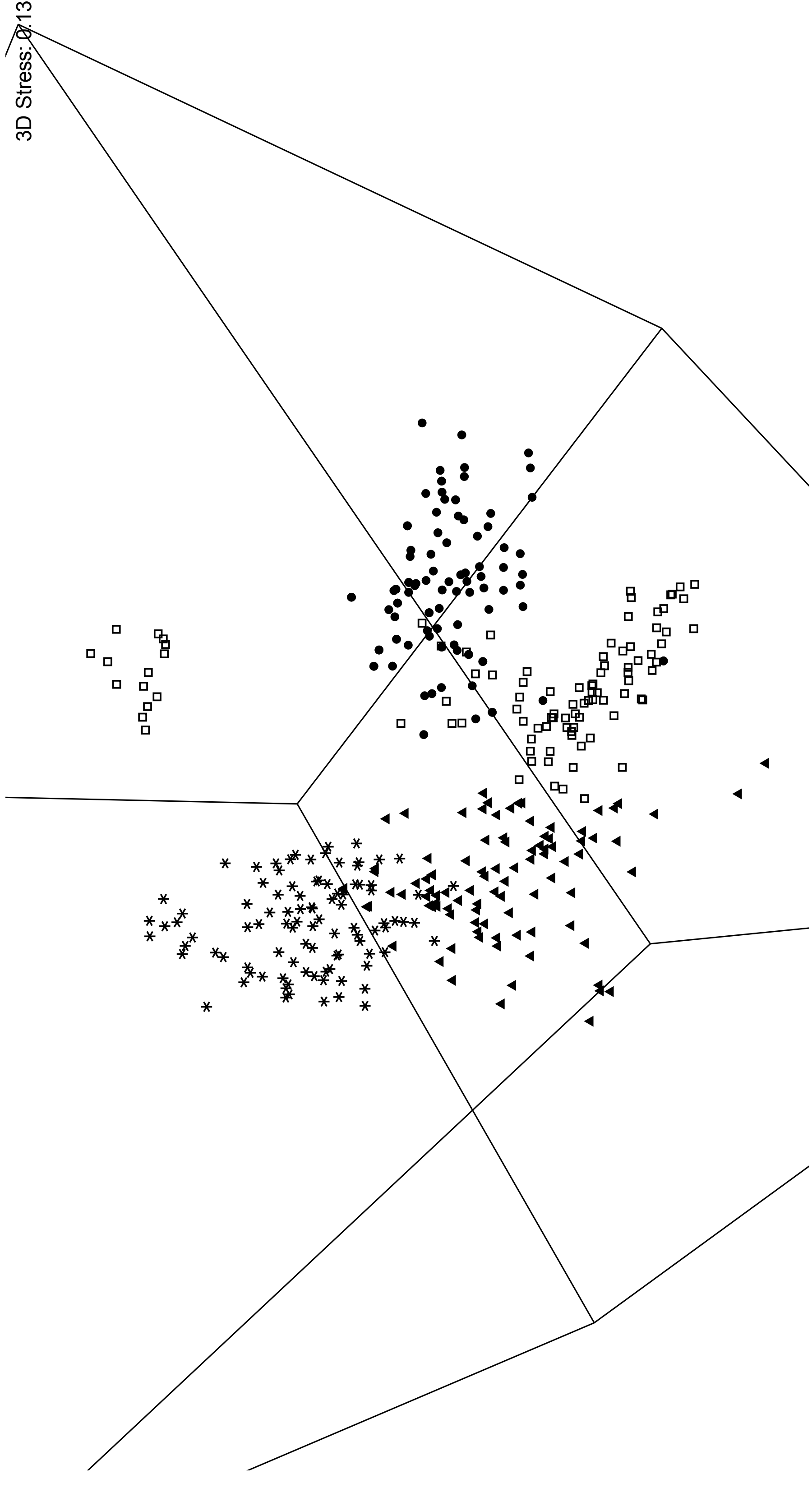
Appendix 13

Cluster analysis of dunging species abundance and SIMPROF analysis. Grouping labels: A-N= (W) woodland, O-W = (G) grassland, X-AI = (H) heath, AJ-AS = (M) mire.



Appendix 14

Three-dimensional ordination plot for non-metric multidimensional scaling of dunging species composition plots for all habitats. ▲Grassland, □ Heath, ● Mire, ✱ Woodland.



Appendix 15

T-test analysis between key species abundance controls (wormed and natural controls) for each factor combination. * denotes a significant difference (P<0.01); where no result is provided species were not present and the mean and variances were equal to 0.

	Grassland		Heath		Mire		Woodland	
	Horse	Cattle	Horse	Cattle	Horse	Cattle	Horse	Cattle
Agrostis	2.527*	0.153	1.653	3.663*	0.754	0.516	2.236*	0.826
Juncus	0.050	1.616	0.160	0.499	1.586	1.565	1.164	0.238
Molinia	0.482	1.667	2.169*	0.061	1.629	0.230	1.215	0.705
Carex	0.547	0.711	2.603*	3.070*	0.731	0.930	2.622*	0.086
Calluna	1.000	1.599	0.802	0.344	1.817	0.633	1.000	-

Appendix 16

SIMPROF test between dunging species compositions (Bray-Curtis similarity) from 999 simulation permutations. Percentage similarities (%), Pi: (Significance level <5%)

Points of delineation	
47+96 -> 97 at 97.72	38+139 -> 145 at **73.49**
17+73 -> 98 at 97.55	124+138 -> 146 at **73.12**
3+19 -> 99 at 97.37**; Pi: 0 Sig(%): 100**	83+140 -> 147 at **72.93**
62+67 -> 100 at 97.08	87+88 -> 148 at **72.86**
59+71 -> 101 at 96.97**; Pi: 0 Sig(%): 100**	2+141 -> 149 at **72.8**; Pi: 3.24 Sig(%): 1.9
60+72 -> 102 at 96.83**; Pi: 0 Sig(%): 100**	114+132 -> 150 at **72.63**; Pi: 2.08 Sig(%): 1.4
32+46 -> 103 at 96.27**; Pi: 0 Sig(%): 100**	126+147 -> 151 at **72.23**
63+68 -> 104 at 94.06**; Pi: 0 Sig(%): 100**	101+102 -> 152 at **72.09**; Pi: 8.64 Sig(%): 0.1
8+24 -> 105 at 93.51	51+144 -> 153 at **71.8**
89+98 -> 106 at 93.25**; Pi: 0.78 Sig(%): 24.9**	130+150 -> 154 at **71.45**; Pi: 1.98 Sig(%): 0.1
53+65 -> 107 at 91.59**; Pi: 0 Sig(%): 100**	11+12 -> 155 at **71.35**; Pi: 0 Sig(%): 100
27+29 -> 108 at 90.62	58+152 -> 156 at **70.72**; Pi: 6.09 Sig(%): 0.1
49+69 -> 109 at 90.01**; Pi: 0 Sig(%): 100**	37+131 -> 157 at **70.32**
44+76 -> 110 at 87.72**; Pi: 0 Sig(%): 100**	15+16 -> 158 at **69.8**
21+22 -> 111 at 87.12	146+157 -> 159 at **69.63**
43+108 -> 112 at 86.85	143+148 -> 160 at **69.42**
54+66 -> 113 at 86.83**; Pi: 0 Sig(%): 100**	153+159 -> 161 at **68.78**; Pi: 0.48 Sig(%): 58.5
92+103 -> 114 at 86.69**; Pi: 2.29 Sig(%): 1.9**	145+151 -> 162 at **68.54**
7+23 -> 115 at 86.63	109+149 -> 163 at **68.25**; Pi: 2.64 Sig(%): 0.6
50+70 -> 116 at 85.89**; Pi: 0 Sig(%): 100**	13+104 -> 164 at **67.45**; Pi: 8.87 Sig(%): 0.1
31+74 -> 117 at 85.78	75+154 -> 165 at **67.02**; Pi: 1.71 Sig(%): 0.4
39+93 -> 118 at 85.35	57+156 -> 166 at **66.89**; Pi: 4.55 Sig(%): 0.1
18+78 -> 119 at 85.15	10+158 -> 167 at **66.81**
4+20 -> 120 at 85.04**; Pi: 0 Sig(%): 100**	1+162 -> 168 at **66.45**
28+97 -> 121 at 84.53	9+100 -> 169 at **66.34**
79+105 -> 122 at 83.88	26+163 -> 170 at **66.3**; Pi: 2.19 Sig(%): 1.6
42+106 -> 123 at 82.06**; Pi: 2.96 Sig(%): 2**	161+165 -> 171 at **66.19**; Pi: 0.69 Sig(%): 3.9
94+118 -> 124 at 81.96	81+168 -> 172 at **65.33**; Pi: 0.79 Sig(%): 13
48+121 -> 125 at 80.92	99+170 -> 173 at **64.29**; Pi: 2.5 Sig(%): 0.2
34+36 -> 126 at 80.54	113+171 -> 174 at **63.79**; Pi: 0.71 Sig(%): 3.4
111+119 -> 127 at 80.32	116+166 -> 175 at **63.76**; Pi: 3.43 Sig(%): 0.1
33+117 -> 128 at 80.06	64+164 -> 176 at **63.64**; Pi: 5.88 Sig(%): 0.1
6+122 -> 129 at 78.87	61+176 -> 177 at **63.21**; Pi: 3.63 Sig(%): 2.2
91+123 -> 130 at 78.67**; Pi: 3.33 Sig(%): 1.2**	160+167 -> 178 at **62.59**
115+127 -> 131 at 78.57	120+172 -> 179 at **61.58**; Pi: 1.19 Sig(%): 2.3
80+129 -> 132 at 78.51**; Pi: 1.42 Sig(%): 10**	155+175 -> 180 at **61.06**; Pi: 2.43 Sig(%): 0.1
5+45 -> 133 at 78.49	169+178 -> 181 at **60.21**; Pi: 1.08 Sig(%): 16.3
85+86 -> 134 at 78.08	179+181 -> 182 at **59.88**; Pi: 1.3 Sig(%): 0.4
77+128 -> 135 at 77.83	41+142 -> 183 at **58.69**; Pi: 4.85 Sig(%): 0.3
25+112 -> 136 at 77.43	52+180 -> 184 at **58.07**; Pi: 2.2 Sig(%): 0.1
56+134 -> 137 at 76.76	173+182 -> 185 at **57.03**; Pi: 1.3 Sig(%): 0.1
90+133 -> 138 at 75.87	174+185 -> 186 at **55.17**; Pi: 2.15 Sig(%): 0.1
40+82 -> 139 at 75.62	84+184 -> 187 at **55.03**; Pi: 2.22 Sig(%): 0.1
125+135 -> 140 at 75.21	177+186 -> 188 at **53**; Pi: 1.8 Sig(%): 0.1
30+107 -> 141 at 74.92**; Pi: 4.69 Sig(%): 0.5**	187+188 -> 189 at **50.07**; Pi: 1.95 Sig(%): 0.1
95+136 -> 142 at 74.62**; Pi: 2.1 Sig(%): 8.5**	110+189 -> 190 at **29.03**; Pi: 2.29 Sig(%): 0.1
14+35 -> 143 at 74.3	183+190 -> 191 at **25.62**; Pi: 3.8 Sig(%): 0.1
55+137 -> 144 at 73.98	

Glossary of terms

Analysis of Covariance (ANCOVA) – ANCOVA is a statistical procedure that enables one to compare groups on some quantitative dependent variable while simultaneously controlling for quantitative independent variables. The test effectively uses a regression analysis to remove the effect of the covariate before the standard ANOVA is attempted.

Analysis of Variance (ANOVA) – a collection of models used to test the hypothesis that variation in the response variable *Y* can be partitioned into different levels of one or more explanatory *X* variable(s). It is an appropriate analysis method for a study with a quantitative outcome and one (or more) categorical explanatory variables.

Arcsine transformation - transformation traditionally used for proportions (which range from 0.00 to 1.00), the calculation is based on taking the arcsine of the square root of a number, with the resulting transformed data reported in radians.

Box-Cox transformation – a continuum of transformations that provide a range of opportunities for closely calibrating a transformation to the needs of the data,

$$y_t^{\lambda} = \log_e(y_i),$$

where $\lambda = 0.1$.

Bray-Curtis distance - statistic used to quantify the compositional dissimilarity of groupings or sites for ordinations (Clarke and Gorley, 2006):

$$BC_{\mathrm{ij}} = \frac{2C_{ij}}{S_i + S_j}$$

where C_{ij} is the sum of the lesser value for only those species in common between both sites. S_i and S_j are the total number of specimens counted at both sites.

Chi-square test - a contingency table-based statistical test to explore hypotheses of association between variables; expected values are generated by the table.

Cluster analysis – a number of multivariate tests that group observations by similarity to provide insight into the data under examination.

Comparative Dunging Intensity (CDI) - a calculated index first used to indicate preference or avoidance of areas, but also used as an indicator of aggregation in herbivores (Bakker et al., 1983). Calculated by:

$$\mathrm{CDI} = \frac{A}{a} \times \frac{\mathrm{d}(t_2 - t_1)}{D(t_2 - t_1)} - 1$$

where A = entire study area (m^2); a = sampled area in section a (m^2); d = amount of dung in the sampled area in a (ml) accumulated over the period (t_2 - t_1); D = amount of dung in the entire study area (ml) accumulated over the period (t_2 - t_1).

Dietary overlap – measure of overlap of proportional diet between horses and cattle, calculated using **Kulczinski's similarity index** (in this study) – a similarity coefficient calculated using the equation,

$$\alpha_{\mathrm{hc}} = \sum \min(p_{ih}, p_{ic}),$$

where p_{ih} and p_{ic} are the proportions of the grazing time that horses and cattle spent foraging on *i*th food type.

Foliage Height Diversity (FHD) Index - Similar to the Shannon-Weiner diversity index, the FHD index uses richness and evenness to assess the diversity of the vertical distribution of foliage

$$-\sum_{\mathrm{i}} (p_{\mathrm{i}} \, log_{\mathrm{e}} \, p_{\mathrm{i}}),$$

where p_i is the proportion of vegetation found in the *i*th strata

Forbs - herbaceous species (esp. a pasture plant other than grasses)

***F*-ratio** – the statistic calculated from parametric analyses of variance which reveals the significance that the dependent variable depends on the independent variable. It is the ratio of the variance between the treatments and the variance within the treatments.

Functional response - the relationship between intake rate and forage availability is known as the functional response, first derived as a model of predator-prey interactions by Holling (1959)

Generalized Linear Model - a parametric framework which relies on making assumptions about other distributions of data that are not normal. The Generalized Linear Model can also cope with non-scale response variables where assumptions of normality and/or homogeneity cannot be met. The three characteristics of the model are: a response variable at its probability distribution (e.g. Poisson, binomial), a set of explanatory variables and an error term (i.e. the linear predictor), and a link function connecting the above two (e.g. log link function).

Graminoids – grasses and grass-like forms, including grasses, sedges, rushes

Homogeneity of regression slopes - An assumption of ANCOVA that the covariate regression slopes are parallel for each group, or each group has covariate regression slope that is similar.

Kolmogorov-Smirnov (K-S) two-sample test: a non-parametric test that compares two distributions.

Log-likelihood statistic – alternative statistic to chi-square statistic, used to test for overall significant selection of resources. It is appropriate for proportions of available units in different resource categories when they are known. It tested if overall selection was proportional to availability (Manly et al., 2002)

$$X_L^2 = 2 \sum u_i \log_e \{u_i / (u_+ \pi_i)\},$$

where u_i is the sample count (proportion habitat used),
π_i is the population proportion (proportion of habitat available).

Log transformations - a series of transformations which use the logarithm, the power (exponent) a base number must be raised in order to get to the original number.

Manly's selection index - (B_i) estimates proportional habitat selection, and is interpreted as being the estimated probability that a category *i* resource unit (habitat type) would be the next one selected if it was possible to make each of the resource types equally available.

$$B_i \ = \hat{w}_i/(\sum_{i=1}^{1} \hat{w}_j$$

where $\hat{w}_i = o_i/\pi_i$, the selection ratio, $o_i = u_i/u_+$, sample proportion of used units, π_i = proportion of the population of available units that are in category *i,* u_i = number of units in category *i* in a sample of used units, u_+ = size of sample of used resource units.

Mesic – typical habitat type of moderately moist temperate climate

Microsite – the micro-level site of colonisation within a sward, often within an environment with unique features, conditions or characteristics

Niche breadth – measure breadth of habitat use or diet by each animal:

$$B_A = B\text{-}1 / n\text{-}1,$$

where *B* is breadth and *n* is the number of habitat types, derived from Levins' measure of niche breadth ($B = 1/\sum p_i^2$, where p_i is the proportion of selections in habitat *i*).

Niche overlap – measure of the overlap of proportional use of habitat by horses and cattle, calculated using **Pianka's index,**

$$O_{hc} = \{\Sigma\ (p_{ih} * \ p_{ic})\}`/\{\ (\Sigma\, p_{ih}{}^2 * \Sigma\, p_{ic}{}^2)^{0.5}\},$$

where p_{ih} and p_{ic} are the mean proportional habitat use by horses and cattle

Non-metric multidimensional scaling (MDS) - Multidimensional scaling (MDS) is a series of techniques that assists in identifying key dimensions or underlying trends in objects. The main objective of MDS is to represent dissimilarities between these objects as distances between points in a low dimensional space such that the distances correspond as closely as possible to the dissimilarities. It is numerical technique that iteratively seeks a solution and stops computation when an acceptable solution has been found, or it stops after some pre-specified number of attempts. Unlike PCA, which assumes linear relationships, MDS does not make these assumptions so it is widely useful for many types of data – for graphical representation

Ordination – a method complementary to data clustering, and used mainly in exploratory data analysis (rather than in hypothesis testing). The approach orders objects characterized by values based on multiple variables (i.e. multivariate objects) so that similar objects are near each other and dissimilar objects are farther from each other.
Palaeoecology – the study of the relationship between past organisms and the environment in which they lived.

Podsol – grey forest soil, the soil of cold temperate regions, and formed on heathlands and under coniferous forest

Podsolisation – the process of the formation of grey soils under some forests and heathlands, generally in areas where precipitation is greater than evapotranspiration, and minerals are removed by leaching. Acidification often occurs in these circumstances as organic acids are released from decomposition.

Poisson distribution – a discrete probability distribution that expresses the probability of a given number of events occurring in a fixed interval of time and/or space.

***P*-value** – the *P* value reflects the probability of getting a value, for the calculated statistic, equal to or more extreme than the one calculated in a hypothesis test, if the null hypothesis is true. It is a measure of the significance, or the probability of mistakenly rejecting the null hypothesis that is actually true.

Regression – a description of the relationship between two variables where the value of one (dependent 'effect' variable) is determined by the value of the other (independent 'cause' variable)

***R*-squared – the amount of variation explained in the dependent variable based on the independent variable.** The *R-square* value is an indicator of how well the model fits the data (e.g., an *R-square* close to 1.0 indicates that we have accounted for almost all of the variability with the variables specified in the model)

Resource partitioning *(or* niche differentiation) – the mechanism by which animals can co-exist (e.g. grazers) by utilising different resources within the same area

Shannon-Wiener diversity index – measure of species diversity based on species richness and the evenness of the species, calculated by:

$$H' = - \sum p_i \ln p_i ,$$

where p_i = the proportion of individuals of species i.

Sidak I-J (post hoc test) – also called the Dunn-Sidak test, a post-hoc test used after a one-way ANOVA to determine which groups are different from which.

SIMPROF test – (similarity profile) permutation method which tests for significance of groupings in a cluster analysis or for structure in the data after making a similarity profile by ranking the similarity matrix (in PRIMER). A mean profile is then calculated by randomising the order of each variable value and re-calculating the profile. The *Pi* statistic is calculated as the deviation of the actual data profile from the mean one. This is compared with the deviations of further randomly generated profiles to test for significance (Clarke and Warwick, 2001).

Square-root transformation – square root of every value is taken from positive values (if negative numbers are present a constant must be added to all)

Stocking density – calculation of livestock units per hectare

***T*-test -** compares between two means to suggest whether both samples come from the same population; parametric assumptions apply.

Type II Functional Response - the rate at which consumption increases as food availability increases gradually declines until a plateau is reached, normally observed in herbivores.

Variance – the sum of squared deviations of observations from the mean; a measure of spread of the data.

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