Investigating the drivers of spatial and temporal biodiversity patterns of the Machair

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Declaration of work carried out

I declare that the work presented in this thesis, which was conducted in part at the James Hutton Institute (formerly known as the Macaulay Land Use Research Institute), and at the School of Environmental Sciences, University of Liverpool, is my own, and has not been accepted in any previous application for a degree. All sources of information have been specifically acknowledged. This thesis is submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor of Philosophy.

Work in Chapters Two, Three, Four and Five in this thesis is wholly or in part based on data collected as part of the Scottish Coastal Survey between (1975 and 1977) contracted at the time by the Nature Conservancy Council (NCC) and Institute of Terrestrial Ecology (ITE). Fieldwork involving a vegetation re-survey of the baseline data was undertaken and overseen by the James Hutton Institute, involving a principal research team (Robin Pakeman; Richard Hewison; Roger Cummins and Ruth Mitchell) and full-time students (Clare Pemberton; Emily Moore; Katy Orford and Sarah Gore).

Work in Chapter Four involved the use of a functional trait database developed by Dr Rob Brooker, James Hutton Institute. Dr Jack Lennon, University of Belfast, developed the climate indices used in Chapter Five.

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Dedication

For

Grandma (The late Elizabeth Charlotte Lewis)	Grandad (The late David Brian Lewis)

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Summary

In plant ecology, understanding which species live where and why is fundamental for ensuring successful conservation management with the aim of maintaining biodiversity and ecosystem services. Biodiversity patterns in space can be empirically linked to spatially scaled environmental processes, providing a greater understanding to how plant species assemblages change along differing environmental gradients. In the same way, biodiversity patterns in time can be linked to temporal trends in the environment, empirically linking changes in vegetation to changes in the external environment. This furthers understanding of how plant communities are likely to respond to future scenarios of environmental change, providing an insight into future shifts in biodiversity patterns and, in turn, how his may influence valuable ecosystem functions and services upon which humans ultimately depend.

Trends in human land use have been shown to be the single most influential driver of current global biodiversity change to date. This, coupled with a changing climate, suggests vegetation communities on a global scale are under increasing pressure to adapt to multiple dynamically changing environmental constraints. This thesis focuses on a globally-rare semi-natural, coastal grassland habitat termed 'Machair', renowned for its high biodiversity and cultural heritage importance. Confined solely to the north-western fringe of Europe, the Machairs have formed through unique combinations of geo-physiological and climatic conditions, and even more importantly, century-long associations with human land use through which the low-intensity intermediate disturbance is considered to be vital in maintaining its biodiversity value. However, change in the management of the Machairs alongside other environmental drivers of change, particularly climate, provides major concerns for the biodiversity value of this habitat.

In this thesis, spatial and temporal biodiversity patterns of Machair vegetation are investigated to assess the major drivers of change and identify regions which may require future conservation efforts to restore and/or maintain the future biodiversity value of this globally-rare habitat. To achieve this, a spatio-temporal dataset of Scottish Machair vegetation first collected in 1976-77 and then re-surveyed in 2009-10 was used. Analyses found both climate and land use management to influence spatial and temporal vegetation patterns of Scotland's Machair and Machair grassland. Climate was shown to operate at relatively broad scales (>50km), while the influence of different measurable components of climate was also found to significantly affect temporal turnover patterns of Machair grassland assemblages.

Land use management, predominantly at a relatively fine scale (<1.5km), is shown to be the single most influential driver of spatial turnover patterns among both the national extent of Scotland's soft coast habitats (i.e. low lying coastal areas composed of sand, shingle or mud) and Machair. This

indicates the relative importance of land use management in maintaining the high habitat heterogeneity and a high proportion of edge habitat believed to be vital for maintaining the high biodiversity value typical of these habitats. Considerable change in Machair biodiversity for many of Scotland's regions was observed, much of which could be reasonably well linked to reported shifts in land use, particularly shifts towards increased use of inorganic fertilisers and either increased or decreased agricultural intensification. Not all change was deleterious, many regions which were once included in government incentivised schemes specific to the protection and biodiversity maintenance of Machair grassland displayed higher biodiversity, including species of conservation importance. This highlights the importance of financial incentives to encourage environmentally sensitive land use management more inline with traditional practices, which are increasingly becoming socially and economically unviable.

The analyses used were deliberately targeted to identify the community assembly processes by which the Machair communities are governed at local, regional and national scales. It is evident that these communities are governed by environmental filtering at relatively broad regional scales principally through climatic constraints, and similarly at relatively fine local scales through constraints imposed by land use management. It is also evident that community assembly processes are not mutually exclusive and operate simultaneously, at hierarchical scales. Biotic processes at extremely fine scales certainly operate to govern the vegetation communities of Machair grasslands, evident through functional trait divergence. Furthermore, shifts in land use management are shown to impact on these assembly processes, displaying for several regions, an increase in constraints through environmental filtering and reduced resilience through reduced niche differentiation.

This study makes a valuable contribution to knowledge of how land use and climate impact on spatial and temporal biodiversity patterns among Machair vegetation, identifying the relative importance of climate and land use determinants, the scale at which they operate, and, how current trends are influencing the biodiversity value of the Machairs at national and regional scales. Furthermore this research demonstrates the utility of different methodological advances and techniques in investigating patterns of biodiversity change for a better understanding of the patterns and processes that govern plant communities.

Contents

Chapter One

General Introduction

Spatial and temporal variability in biological diversity (i.e. biodiversity) is a fundamental property of ecological systems. Since the birth of modern biogeography (Darwin 1859; Wallace 1870), researchers have examined patterns of species distributions, in an attempt to understand the mechanisms that generate and maintain this variation. In the realm of plant ecology, a connection between the physical and biotic environment and species distribution patterns was established early on (Cowles 1899). Nevertheless understanding the ecological and physiological processes by which species assemble themselves into communities is still a major focus for ecological research and has invoked many theories of species coexistence and community assembly.

These theories broadly unify ideas of area, richness and abundance, e.g. species-area relationship (SAR) and species abundance distributions (SAD) into at least 6 different theories of biodiversity (see McGill 2010 for full review). However, many studies focus principally on niche-based environmental filtering and limiting similarity (Cornwell et al. 2006; De Bello et al. 2009; Mason et al. 2011) and species-neutral processes as competing explanations for community assembly (McGill et al. 2006).

Niche theory suggests that assembly processes filter (i.e. restrict) the range of species with differing phenotypic properties under different abiotic environmental conditions, resulting in a convergence of coexisting species, expressing greater similarity than would be expected by chance (Zobel 1997). Here community assembly leads to a single-state equilibrium, where regions of local communities with similar environmental conditions should have similar community composition (Chase 2003). In contrast, biotic processes such as competitive exclusion (Hardin 1960; Grime 1973) predict a limit to the similarity of coexisting species (MacArthur and Levins 1967) and assume the stable coexistence of functionally dissimilar species. Here community assembly leads to multiple state equilibria, where regions of local communities with similar environmental conditions can potentially have very different community composition (Chase 2003). There is also the possibility that communities assemble under neutral processes (Hubbell 2001), which suggests that species and individuals are equivalent, and thus coexist independently of their functional characteristics. In other words the processes that determine species assembly are wholly stochastic and unmeasurable. Hubbell (2001) distinguished dispersal-assembly rules, apart from abiotic and biotic assembly, arguing that dispersal processes alone explain most of the variation in biodiversity patterns of trees in forests.

Arguably, spatial and temporal patterns of plant community assemblages are the result of all three processes operating at different spatial scales. At the broadest scale, local species pools recruit species from the regional species pool through dispersal assembly. Thereafter, abiotic filters and at the finest scale, biotic interactions, define the actual assemblage of plant species (Zobel 1997, Gotzenberger et al. 2012). Nevertheless, the question remains whether any single assembly process is generally dominant or whether the influence of contrasting processes varies in a predictable way relative to biotic and abiotic gradients (Mason et al. 2011).

Understanding how communities are structured should allow a greater insight into the dynamic processes governing spatial and temporal patterns of species composition, and *vice-versa*. Moreover, disentangling the different processes involved in community assembly is crucial for an understanding of how communities may behave under future environmental scenarios, particularly changes in climate, resource availability and/or management. From a biodiversity conservation perspective, this is of upmost importance, as only if we know in some detail how species and individuals persist in the environment can we successfully develop and implement conservation management for attempts to maintain biodiversity (Grime 2006).

1.2 Drivers of biodiversity change

Globally, changing land use patterns are a major cause of current unprecedented rates of biodiversity loss (Sala et al. 2000). Predominant changes include land conversion from complex natural ecosystems to simplified agricultural ecosystems (i.e. altered for human use), and agricultural intensification (e.g. greater intensity and/or frequency of disturbance). Such human modification of landscapes is well reported to be directly linked to changes in biodiversity, documenting national and landscape-scale declines in taxonomic diversity of birds (Donald et al. 2001), mammals (Sotherton 1998), insects (Goulson et al. 2010) and plants (Smart et al. 2006) through land alteration.

However, the biological impacts of climate change are also well documented (Parmesan et al. 1999; Parmesan and Yohe 2003; Root et al. 2003; Hickling et al. 2006), and in the realm of plant ecology, anthropogenic climatic change can provide the most parsimonious explanation for changes in the physiology, distributions and phenology of many species (Thuiller et al. 2005).

1.3 Biodiversity loss and ecosystem function

Undoubtedly, continued ecological focus on identifying drivers of biodiversity change is in part due to the aforementioned unprecedented rates of biodiversity loss at a global scale (Sala et al. 2000). However, it is also undeniably due to increased recognition of the linkages between biodiversity and ecosystem function, and concerns that biodiversity loss will affect the ecosystem services provided by natural and semi-natural communities (Chapin et al. 2000; Diaz et al. 2007).

Most ecosystems provide goods and services, such as food provision, climate regulation, nutrient cycling, water quality and many more, on which humans ultimately depend (Millennium Ecosystem

Assessment 2005). These services have recently been related to ecosystem biological characteristics, specifically functional traits (Kremen 2005; De Bello et al. 2010). Ecologically, a species is a collection of individuals with phenotypic and behavioural characteristics (i.e. functional traits) that determine their distribution and how they interact with other species (McGill et al. 2006). Changes in the environment can affect the physiology, morphology and behaviour of species, altering the structure of populations and ultimately community composition (Suding et al. 2004). In this context, there is a growing consensus that functional trait diversity is more informative than taxonomic diversity *per se* in explaining the structure and function of ecological communities (McGill et al. 2006; Mokany et al. 2008), and is reshaping how ecologist measure biodiversity, assess coexistence and restore habitats (Cadotte et al. 2011).

1.4 Detecting Biodiversity Loss

The focus of conservation policy in response to environmental change is to mitigate against biodiversity loss. Successful conservation management does, however, require detailed knowledge of spatial and, importantly, temporal patterns of biodiversity, often across large geographical regions (Margules and Pressey 2000). However, large-scale temporal datasets are often scarce, particularly on a national-scale where sampling often results in extensive areas left un-surveyed. Moreover, temporal datasets, necessary for the identification of temporal shifts in biodiversity in response to environmental change in time, are very rarely available, and extremely scarce at regional and national scales, resulting in few attempts to quantify large-scale changes in biodiversity (Thomas et al. 2004). As a result, methods used to track changes in biodiversity often combine information on the status of individual species to provide an overview of change, as, for example, the Living Planet Index (Loh et al. 2005). However, these indices have the disadvantage that conclusions are made on the basis of a non-random selection of species (Magurran and Henderson 2010).

It is clear therefore, that the monitoring of changes in biodiversity in relation to baseline data has the potential to provide solid empirical links between biodiversity and, ecosystem functions. Nevertheless, much research on species turnover has focused on spatial rather than temporal patterns (Magurran 2007). This is in most part due to the lack of available long-term temporal data, as mentioned above, and highlights both the need for baseline biodiversity data to establish levels from which to assess and evaluate change, and also, how little empirical information are available on how biodiversity changes through time.

1.5 Baseline biodiversity data

Here, baseline data to analyse spatial and temporal biodiversity patterns are derived from the Scottish Coastal Survey, undertaken between 1975 and 1977. Increased pressure of recreational activities and industrial developments during the mid 1970s highlighted a lack of information on important Scottish coastal habitats (Shaw et al. 1983). With the aim of identifying the ecologically important and sensitive areas of Scotland's soft coast (i.e. low lying coastal areas composed of sand, shingle or mud) the then Nature Conservancy Council (NCC)[1] commissioned the then Institute of Terrestrial Ecology (ITE)[2] to conduct a national-scale survey of Scottish soft coast areas. This survey is referred to hereafter as the Scottish Coastal Survey; it was carried out by teams of trained surveyors recording data on plants, habitats, environment and land use of circa 4000 randomly located vegetation plots between 1975 and 1977.

In total, 94 sites were surveyed, within which circa 4000 plots were located, spanning the coastline of Scotland (Fig. 1.1). Habitats include the relatively lime-poor, acidic substrates of the east coasts, where succession results in dwarf shrub communities with *Salix repens*, *Erica tetralix*, *Empetrum nigrum* and *Calluna vulgaris* dominate (Welch 1989), to the hyper-oceanic calcareous dune systems occurring on the Western Isles, including the species-rich grasslands of the Machair. Defined by various authors as an extremely complex, species-rich costal dune plain (Angus and Dargie 2002; Kent et al. 2003; Angus 2006), Machair grasslands are renowned for their rarity and high floristic diversity. Temporal biodiversity patterns were assessed through a re-survey of only those sites known to include such Machair biotypes, providing temporal data for most of the western seaboard and the North coast of Scotland, including Orkney and the Shetland Isles (Fig. 1.1).

1.6 The biodiversity importance of soft coast habitats

The results presented in Chapter 2 of this thesis are based solely on data from the Scottish Coastal Survey, encompassing almost the entire national resource of Scotland's soft coasts. These habitats, in particular the coastal dunes, are renowned for their high ecological diversity. The semi-natural open dune grasslands that typically lie behind the pioneer vegetation of the embryo and mobile dunes are among the most species-rich plant communities in Central and Northwest Europe. However, they are also among the most vulnerable, with reported declines in area of 40% since 1900 and by a further one third since the late 1970s (O'Briain 2005). Therefore, coastal dune systems have been included as priority habitat types of the European Habitats Directive 92/43/EEC (Council of the European Commission 1992).

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[1] NCC has since been split into separate government agencies. The current agency responsible for the management of Scottish coats is Scottish Natural Heritage (SNH).

[2] ITE is now the Centre of Ecology and Hydrology (CEH).

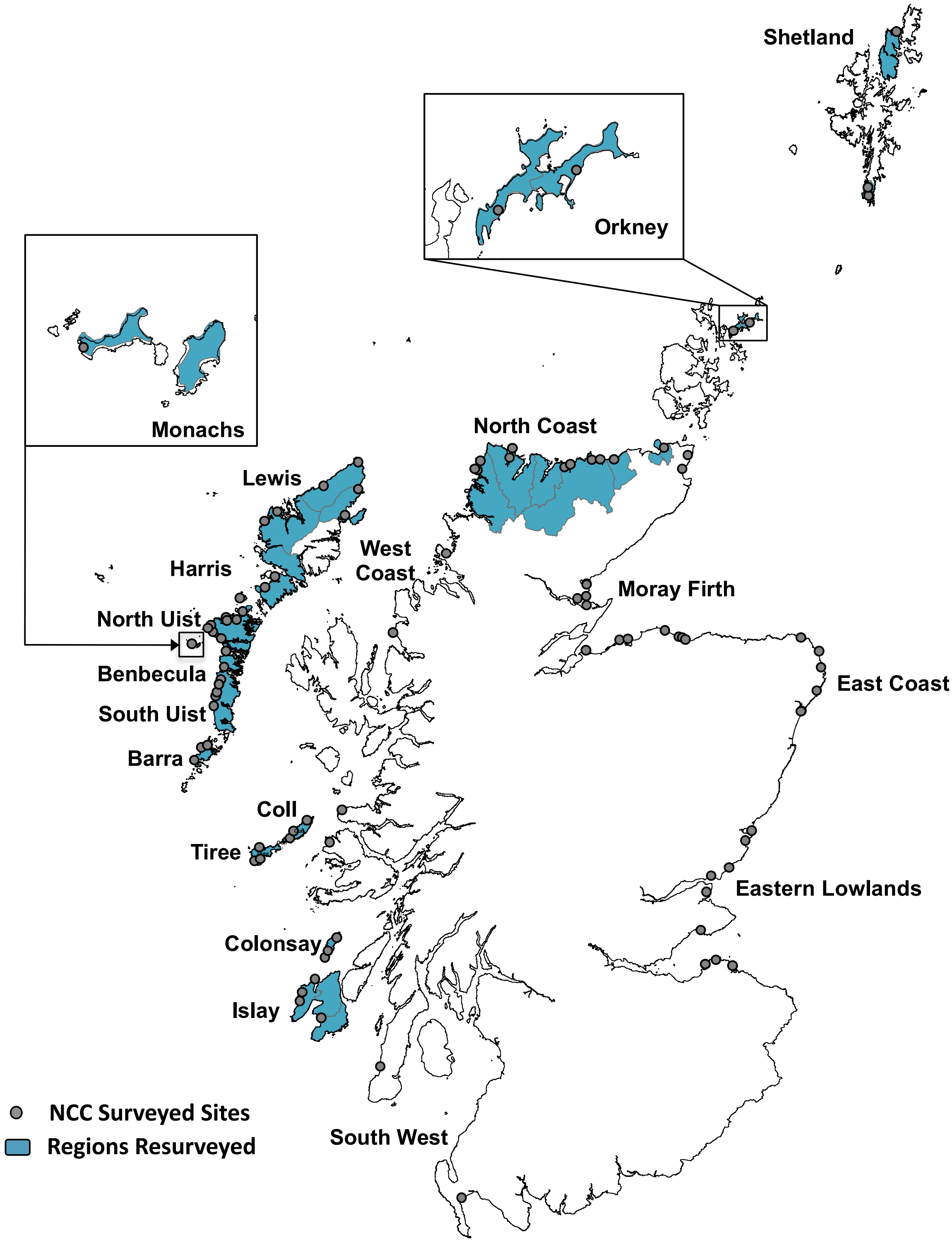


Fig. 1.1 Site locations as selected by the Nature Conservancy Council (NCC). Sites within regions shaded blue indicates those sites re-surveyed. Selection criteria for re-survey were based on regions known to support Machair grasslands, a globally-rare, and floristically diverse habitat.

As with many natural ecosystems worldwide, coastal dune systems are threatened by land conversion through human activities e.g. agriculture, recreation and development (Doody et al. 1993; van der Maarel and Usher 1997; Heslenfeld et al. 2004). However, the principal threat to most existing dune systems is over-stabilisation, where the dynamism of early successional species-rich grasslands are replaced by later successional scrub and woodland vegetation (Westhoff 1989; Houston 1997). Shifting from open grassland to later successional states is often perceived as a serious threat to biodiversity and is well reported to be deleterious to many species, reducing plant species richness (Rejmánek and Rosén 1992; Alvarez and Cushman 2002), although not unequivocal (Isermann et al. 2007). The process is in part attributable to deliberate stabilisation efforts i.e. afforestation (Ovington 1950) and planting of *Ammophila arenaria* (Hewett 1970), and also increased atmospheric deposition of nutrients in some regions (Jones et al. 2008). However for most, it is a direct result of significant declines in grazing by rabbits and domestic stock (Doody 1989).

1.7 International importance of Scotland's soft coast habitats

Scotland's coasts hold over 70% of the UK's entire coastal dune resource, much of which is considered to be in good condition compared with other mainland European countries (Angus et al. 2011). Scotland's soft coast habitats also hold international conservation status. Machair, (defined above) is confined solely to the north-western fringe of Europe. With a total global extent of ca. 40,000 ha, the north-western seaboard of Scotland holds over two thirds (30,000ha) of this globally-rare habitat (Dargie 2000; Anon. 2008), the remaining area being found only in western Ireland (Bassett and Curtis 1985).

In recognition of their rarity and unique conservation importance, Scottish Machair habitats are designated within the suite of Natura 2000 sites, including Sites of Special Scientific Interest (SSSI), Special Area of Conservation (SAC) and Special Protection Area (SPA), and listed on Annex I of the EU Habitats Directive 92/43/EEC (Council of the European Commission 1992). Therefore Scotland has a special responsibility for the conservation of its soft coast habitats.

1.8 Description and biodiversity value of Machair

Strictly the term *'Machair*' derived from the Gaelic word *mach*, meaning plain, refers specifically to the low-lying species-rich grasslands that typically lie behind the dune ridge (Angus 1997, 2001). However the term '*Machair'* has been, and often is used interchangeably to refer to the whole system and is best envisaged as a series of transient habitats from seaward embryo dunes to inland sand-affected peatlands termed *blacklands* (Boorman 1993). They comprise a range of habitats in-between from: mobile foredunes, species-rich Machair grasslands, dune slacks, fens and Machair lochs and collectively are termed the '*Machair system'* (Angus 1994). Throughout this thesis, the term

'Machair', if not stated otherwise, is used loosely to refer to the whole Machair system. To avoid confusion, hereafter the Machair plain is referred to as the 'Machair grassland'.

The Machair and its associated landforms are formed through unique combination of sandy calcareous soils, hyper-oceanic climate and relatively extensive, yet low-intensity agricultural practices. The latter are of particular importance, as human populations have played a significant role in shaping the origin and development of Machair systems, with evidence of anthropogenic activity in the form of low-intensity agricultural practices dating back to Neolithic times (Ritchie 1976; Owen et al. 1996). Therefore, Machair systems have a deeply-rooted cultural heritage value with over 2000 years of history linking the landscape and early human settlers. Across many areas of Machair, this cultural heritage is an integral part of the crofting system of land tenure that has developed over the last two centuries.

The high nature conservation value of the Machair grasslands is recognised, at least in part, to result from the extensive, yet low-intensity, agricultural crofting practices (Angus 2009). Traditional cultivation established a rotating pattern of small-scale arable agriculture alongside livestock production. Small strips of land, cropped with black oat *Avena strigosa,* rye *Secale cereale* and barley *Hordeum vulgare* for use as winter fodder, were low-yielding, unfenced and often lay adjacent to fallows of a minimum of 2 years duration (Fig. 1.2a), important in re-establishing nutrients after cultivation (Angus and Dargie 2002; Angus and Hansom 2004). Use of inorganic fertilisers was scarce and cultivation traditionally involved fertilisation with storm-cast marine algae, particularly kelp (*Laminaria hyperborea*).

The result is a small-scale mosaic (typically a few hectares or less) of crops, fallows, grasslands and other habitats with high botanical and invertebrate biodiversity. In contrast to the agricultural intensification that has taken place across much of the rest of the UK and Europe, this form of low-intensity agriculture is understood to promote high biodiversity and abundance within the agricultural landscape. It is therefore unsurprising that agricultural practices have been directly linked to maintaining populations of plant insect and bird species that have declined elsewhere in the UK. For example: plant species common to the Machair fallows, particularly those belonging to the Fabaceae i.e. *Trifolium pratense* and *Vicia cracca*, support stronghold populations of the UK's rarest bumblebee species: *Bombus distinguendus* and *Bombus muscorum* (Benton 2006; Goulson et al. 2005; Redpath et al. 2010). Populations of corncrake *Crex crex* (Fig. 1.2b) and chough *Pyrrhocorax pyrrhocorax*, both Annex I species of the EU Habitats Directives, are promoted through traditional practices of hay stacking, and seasonally-grazed grasslands and peat moorland respectively. Furthermore, the Machair, particularly the Machair grasslands, fallows and lochs are of international significance as both breeding and feeding grounds for large populations of migratory species of waders and wildfowl, including the dunlin, *Caldris alpina*, ringed plover, *Charadrius hiaticula,* Eurasian oystercatcher, *Haematopus ostralegus*, common redshank, *Tringa tetanus*, common snipe, *Gallinago gallinago* and northern lapwing, *Vanellus vanellus* (Fuller et al. 1986; Angus 2001).

1.9 Effects of land use change

In contrast to traditional regimes, socio-economic change within the Machair communities is influencing significantly the way in which land is used. The issues are greatest on the Outer Hebrides, where the Machair is best exemplified (Angus 1996). Here, perhaps of greatest significance is a declining and ageing population, resulting from high outward migration of younger people (Mackenzie 2007). In the crofted areas of the Machair, tenure usually involved multiple tenants within a township. This helped to create an extremely heterogeneous landscape directly linked to the ecological diversity that is characteristic of the Machair. However, an ageing population, and the reduction in the number of active crofters have increased the area of land managed by single individuals (Hansom and Angus 2005; Angus 2009; Osgathorpe et al. 2011). A shift away from small-scale variation in crop and fallow patch size towards larger-scale management, will significantly reduce the heterogeneity of the landscape overall, and the proportion of ‘edge’ habitat per unit area, both of which are believed to promote high biodiversity (McCracken 2009). This is compounded by a fall in the number of active crofters, resulting in a fall in active management of the Machairs. As with all coastal dune systems, Machair and particularly Machair grasslnad requires a level of active management to maintain its biodiversity value. Any relaxation or abandonment in management is usually associated with an increase in tall grasses and forbs (Isermann et al. 2007), highlighting the concern that these species-rich grasslands will become rank and species-poor (Owen et al. 1996; Kent et al. 2003).

These problems are exacerbated by the non-self-sustaining income generated through crofting in an agricultural competitive market (Kent et al. 2003). Traditional crofting practices are therefore becoming increasingly difficult to uphold without government-incentivised income, and are therefore often replaced with less time-consuming and higher intensity approaches.

Fig. 1.2 (a) Traditional reaper-bound haystacks on Ormiclate Machair, South Uist, Outer Hebrides. (**b)** Corncrake *Crex crex* taken on Hebridean Machair.

Pakeman et al. (2011) highlight several concerns with regards to how more recent crofting and farming practices may impact on the conservation value of the Machair. Theses include:

i. Abandonment of traditional rotational cropping and winter grazing regimes for year-round grazing of the in-bye and Machair (Hansom and Angus 2005; Osgathorpe et al. 2011).

ii. Rationalisation of Machair shares leading to management of land in large blocks, instead of traditional strip cultivation (discussed above). Furthermore, larger apportionments of land are increasingly becoming fenced to allow summer grazing on the Machair (Angus 2009).

iii. A shift away from the traditional shallow ploughing towards deeper ploughing practices potentially impacting upon the Machair seed-bank (Owen et al. 2000).

iv. Increased use of inorganic fertilisers in replace of storm cast seaweed.

v. A shift from cattle to less labour-intensive sheep. This reduces labour inputs, but can also reduce overall sward diversity through greater selective grazing by sheep and reduced localised disturbance (i.e. poaching) typically caused by cattle (Love 2009).

A shift in management towards these less intensive practices not only negatively impacts on biodiversity, but may also physically destabilise the Machair grasslands, increasing the threat of habitat loss through erosion. Aeolian processes on the Machair are an essential mechanism contributing to the natural dynamism of these habitats, which in turn promotes species turnover. However, high stocking densities and repetitive grazing, in conjunction with deeper ploughing and a decline in seaweed fertiliser (an important mechanical binding agent for the dune substrate) are believed to have accelerated natural erosion processes. Erosion not only results in habitat loss, but destabilisation of the dunes may increase sand-blow to a level where frequent affect the regrowth of Machair perennials, potentially altering community assemblage composition (Owen et al. 2004). These concerns have particular prevalence in the face of potential climate change, where atmospheric depressions, i.e. high winds and storms are predicted to increase by 40% over the UK by 2080 (Hansom and Angus 2001; Jenkins et al. 2003).

1.10 Potential impact of future climate change

Evidence for changing climatic conditions are well documented both globally and within a UK context (IPCC 2007; Jenkins et al. 2007). Moreover, evidence from long-term monitoring studies is already linking recent climatic variation to the changing physiology, distribution and phenology of several species (Hughes 2000). Although it has been suggested that changing land use may be a more important facilitator of biodiversity change than climate, particularly for grassland ecosystems (Sala et al. 2000), climate change still poses a potential threat, both in its own right and via interactions with other drivers of habitat change (Grime et al. 2008).

In the UK, temperatures have risen by 0.8 - 1.0°C since 1980, and seasonal precipitation patterns have shifted, with much higher winter and lower summer rainfall (Jenkins et al. 2009). These patterns are representative of change in Scotland, with the exception of summer precipitation patterns, where for Scotland they appear to have remained relatively constant (Jenkins et al. 2009).

Much of Scottish Machair, particularly that found on the Outer Hebrides, is associated with hyper-oceanic climatic conditions, where humidity, wind-speeds and precipitation are typically high, and annual temperature range is low (Averis 2000; Angus and Hansom 2004). Increasing temperatures and shifting seasonal precipitation patterns are likely to have a profound effect on the Machair vegetation. Physiological tolerances of temperature and precipitation are governed by the phenotypic properties of individual species (i.e. functional traits), influencing both species distributions and community assemblages. Although evidence linking recent climatic variations to species migrations, typically focus on poleward and upward movement of range-restricted specialists (Walther et al. 2005; Parmesan 2006; Pauli et al. 2012), particularly of alpine species, these processes also apply to community dynamics of the Machair and its associated grasslands. The Machairs, owing to their extreme oceanic climate, are one of the few places in Europe where the ranges of some alpine specialists (e.g. *Arctostaphylos uva-ursi, Polgonum viviparium, Oxyria digyma, Salix herbacea, Saxifraga oppositifolia, Sedum rosea, Silene acaulis*) are relaxed, with populations persisting at near sea-level altitudes (Averis et al. 2000; Angus and Hansom 2004). This phenomenon results from the cold, wet, exposed conditions that inhibit the competitive ability of other species usually common at lower altitudes, thus permitting higher altitudinal species to establish successfully and maintain viable populations.

Shifts in seasonal precipitation patterns towards wetter winters are equally likely to influence change in the vegetation dynamics of the Machair. The greatest change is likely to result from the impact of prolonged winter flooding long into the cultivation season in the following spring. In such instances, standing water will inhibit the management of the Machairs, decreasing environmental heterogeneity, and adversely impacting on biodiversity. Therefore, there are concerns that potential future climate changes will indirectly affect the biodiversity value of the Machair through further discouragement of traditional management that is only just socially and economically viable (Angus and Hansom 2004).

The increased threats of storms and high winds are also likely to result in significant degradation, erosion and loss of valuable Machair habitat, while further loss is threatened through sea-level rise, as with most low-lying coastal systems. In the UK, sea level rose at a rate of 1mm per year during the 20th Century, with rates forecasted to increase under future climate scenarios (Jenkins et al. 2009). However, the extent to which habitat is at risk of, or has suffered degradation or loss falls outside the main scope of this thesis. Here, the focus is specifically on measurable climatic parameters and their ability to influence both spatial patterns (Chapter 2) and temporal patterns (Chapter 5) of Machair species assemblages.

1.11 Aims and Objectives

In the light of current and potential threats to the biodiversity of Scottish Machair systems, this project aimed to assess the extent to which Machair plant community assemblages have changed over the last three decades. A variety of quantitative methods were used to investigate spatial and temporal patterns of both taxonomic and functional diversity. The aim was to assess the utility of such methods for identifying the processes that structure community assemblages applied at the national-scale, with the expectation that a better understanding of the processes that govern which species live where and why will benefit future conservation management for the preservation of biodiversity. Specifically this study addresses the following questions:

- What is the relative importance of land use and climate as drivers of spatial vegetation patterns across Scotland's soft coasts? (Chapter 2).

- How are land use and climatic determinants of Scotland's soft coast spatially scaled, and what can this tell us about the community assembly processes that operate to govern the vegetation assemblages of these communities? (Chapter 2).

- What are the major shifts in plant species assemblages of the Machair system and Machair grassland over 30 years of change, and can changes in land use and climate be linked to changes in vegetation? (Chapter 3).

- Can temporal patterns of plant functional traits help to confirm observed and reported shifts away from traditional land use management among the Machair grasslands? (Chapter 4).

- Can functional trait diversity; measured using Richness, Divergence, Evenness and Dispersion indices help to identify how land use change among Machair grasslands influences community assembly processes? (Chapter 4).

- Is climate important in governing processes of species temporal turnover within the Machair grasslands, and how do different measurable components of climate influence directional change in species richness differences and species replacement components of turnover? (Chapter 5).

- How important are patterns in spatial turnover in capturing patterns in temporal turnover? (Chapter 5).

The approach to answering these questions was principally reliant on the statistical and quantitative methods used for the analysis of data. In order to assess patterns of temporal change (Chapters 3, 4 and 5) a revisitation of Machair grassland sites from the Scottish Coastal Survey was undertaken between 2009 and 2010.

REFERENCES

Alvarez, M.E. and Cushman, J.H. 2002. Community-level consequences of a plant invasion: Effects on three habitats in coastal California. Ecological Applications 12, 1434-1444.

Angus, S. 1994. The conservation importance of the Machair systems of the Scottish islands, with particular reference to the Outer Hebrides. Usher, M.B. and Baxter, J. (Ed.). The islands of Scotland: a living marine heritage, 95-120. HMSO, Edinburgh.

Angus, S. 1996. Natural heritage conservation in the Southern Outer Hebrides. In: Gilbertson, D., Kent, M. and Grattan, J. (eds.) The Outer Hebrides: the last 14,000 years, pp. 227- 250. Sheffield Academic Press, Sheffield.

Angus, S. 1997. The Outer Hebrides: the shaping of the islands. The White Horse Press, Cambridge/Isle of Harris, UK.

Angus, S. 2001. The Outer Hebrides: moor and machair. The White Horse Press, Cambridge/Isle of Harris, UK.

Angus, S. 2006. De tha Machair? Towards a Machair definition. Sand dune Machair 4, 7-22. Aberdeen Institute for Coastal Science and Management, Aberdeen.

Angus, S. 2009. Dé tha cearr air a'mhachaire? Biodiversity issues for Scottish Machair: an initial appraisal. The Glasgow Naturalist 25, Supplement. Machair Conservation: Successes and Challenges, 53-62.

Angus, S. and Dargie, T. 2002. The UK Machair habitat action plan: progress and problems. Botanical Journal of Scotland 54, 63-74.

Angus, S. and Hansom, J.D. 2004. Tir a' Mhachair, Tir nan Loch? Climate change scenarios for Scottish Machair Systems: A wet future? Proceedings Vol.2. Littoral 2004. Delivering sustainable coast: connecting science and policy. 565-569.

Angus, S., Hansom, J. and Rennie, A. 2011. Habitat change on Scotland's coasts. Marrs, S.J., Foster, S., Hendrie, C., Mackey, E.C. and Thompson, D.B.A. (eds) The Changing Nature of Scotland,183-198. TSO, Edinburgh.

Anon. 2008. UK biodiversity action plan priority habitat descriptions: Machair. JNCC. Peterborough.

Averis, A.B.G, Averis, A.M., Horsfield, D. and Thompson, D.B.A. 2000. The upland vegetation of the Western Isles, Scotland. Scottish Natural Heritage. Research, Survey and Monitoring Report, No. 164.

Bassett, J.A. and Curtis, T.G.F. 1985. The nature and occurrence of sand dune machair in Ireland. Proceedings of the Royal Irish Academy 85B, 1-20.

Benton, T. 2006. Bumblebees – The natural history and identification of the species found in Britain. Harper Collins, London.

Boorman, L.A. 1993. Dry coastal ecosystems of Britain: dunes and shingle beaches. In: van der Maarel, E. (ed.) Dry coastal ecosystems Vol. 2A/B. Ecosystems of the World, pp. 197-228. Elsevier, Amsterdam, NL.

Cadotte, M.W., Carscadden, K. and Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48, 1079–1087.

Chapin, F., III, Zavaleta, E., Eviner, V., Naylor, R., Vitousek, P. et al. 2000. Consequences of changing biodiversity. Nature 405, 234–242.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia 136, 489–498.

Cornwell, W.K., Schwilk, D.W. and Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87, 1465–1471.

Cowles, H.C. 1899. The ecological relations of the vegetation of the sand dunes of Lake Michigan. Botanical Gazette 27, 95-117.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray. London.

Dargie, T.C.D. 2000. Sand dune vegetation survey of Scotland: National Report. Scottish National Heritage, Perth.

De Bello, F., Thuiller, W., Leps, J., Choler, P., Clement, J. C. et al. 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. Journal of Vegetation Science 20, 475–486.

De Bello, F., Lavergne, S., Meynard, C.N., Leps, J. and Thuiller, W. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. Journal of Vegetation Science 21, 992–1000.

Diaz, S., Lavorel, S., De Bello, F., Quetier, F., Grigulis, K. and Robson, M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of The National Academy of Sciences 104, 20684–20689.

Donald, P.F., Green, R.E. and Heath, M.F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society B-Biological Sciences London 268, 25–29.

Doody, J.P. 1989. Management for nature conservation. Proceedings of the Royal Society of Edinburgh. Section B-Biological Sciences 96, 247-265.

Doody, J.P., Johnston, C. and Smith, B. (eds) 1993. Directory of the North Sea coastal margin. Joint Nature Conservation Committee, Peterborough, UK.

Fuller, R.J., Reed, T.M., Buxton, N.E., Webb, A., Williams, T.D. and Pienkowski, M.W. 1986. Populations of breeding waders (Charadrii) and their habitats on the crofting lands of the Outer Hebrides. Biological Conservation 37, 333-361.

Gotzenberger, L., de Bello, F., Brathen, K.A., Davison, J., Dubuis, A. et al. 2012. Ecological assembly rules in plant communities-approaches, patterns and prospects. Biological Reviews 87, 111–127.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.E. and Knight, M.E. 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1–8.

Goulson, D., Lepais, O., O'Connor, S., Osborne, J., Sanderson, R.A. et al. 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. Journal of Applied Ecology 47, 1207-1215.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344-347.

Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. Journal of Vegetation Science 17, 255-260.

Grime, J.P., Fridley, J.D., Askew, A.P., Thompson, K., Hodgson, J.G. and Bennet, C.R., 2008. Long term resistance to simulated climate change in an infertile grassland. Proceedings of the National Academy of Sciences 105, 10028-10032.

Hansom, J.D. and Angus, S. 2001. "Tir a' Mhachair (land of the machair): sediment supply and climate change scenarios for the future of the Outer Hebrides machair". In Earth Science and the Natural Heritage of Scotland, Edited by: Gordon, J.E. 68–81. The Stationery Office.

Hansom, J.D. and Angus, S. 2005 Machair nan Eilean Siar (Machair of the Western Isles). Scottish Geographical Journal 121, 401-412.

Heslenfeld, P., Jungerius, P.D. and Klijn, J.A. European coastal dunes: Ecological values, threats, opportunities and policy development. IN: Martinez, M.L. and Putsy, N.P. 2004. Coastal dunes, ecology and conservation. (eds) Springer.

Hardin, G. 1960. The competitive exclusion principle. Science 131, 1292-1297.

Hewett, D. 1970. Colonization of sand dunes after stabilization with marram grass (Ammophila-Arenaria). Journal of Ecology 58, 653–668.

Hickling, R., Roy, D., Hill, J., Fox, R. and Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12, 450–455.

Houston, J. 1997. Conservation management practice on British dune systems. British Wildlife 8, 297–307.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution 15, 56–61.

IPCC. 2007. Climate change 2007. The physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L., (Eds), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 996.

Isermann, M., Diekmann, M and Heemann, S. 2007. Effects of the expansion by Hippophae rhamnoides on plant species richness in coastal dunes. Applied Vegetation Science 10, 33–42.

Jenkins, G., Cooper, C., Hassell, D. and Jones, R. 2003. Scenarios for climate change for islands within the BIC region. Produced for the British-Irish Council by the Meteorological Office, Bracknell.

Jenkins, G.J., Perry, M.C. and Prior, M.J.O. 2007. The climate of the United Kingdom and recent trends. Met Office Hadley Centre, Exeter.

Jenkins GJ, Murphy, J.M., Sexton, D.M.H., Lowe, J.A., Jones, P. and Kilsby, C.G. 2009. UK climate projections: briefing report. Met Office Hadley Centre, Exeter.

Jones, M.L.M., Wallace, H.L., Norris, D., Brittain, S.A., Haria, S. et al. 2008. Changes in vegetation and soil characteristics in coastal sand dunes along a gradient of atmospheric nitrogen deposition. Plant Biology 6, 598-605.

Kent, M., Dargie, T.C.D. and Reid, C. 2003. The management and conservation of machair vegetation. Botanical Journal of Scotland 55, 161-176.

Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? Ecology Letters 8, 468–479.

Loh, J., Green, R.E., Ricketts, T., Lamoreux, J., Jenkins, M., Kapos, V. and Randers, J. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. Philosophical Transactions of the Royal Society B-Biological Sciences 360, 289–295.

Love, J.A. 2009. Oh, dear! What can the Machair be? The Glasgow Naturalist, 25, Supplement. Machair Conservation: Successes and Challenges, 3-10.

MacArthur, R. and Levins. R. 1967. Limiting similarity convergence and divergence of coexisting species. American Naturalist 101, 377

Mackenzie, A.F.D. 2007. The contribution of crofting in the 21st Century. Committee of Inquiry on Crofting. < www.croftingenquiry.org> (accessed 19.01.2012).

Magurran, A.E. 2007. Species abundance distributions over time. Ecology Letters 10, 347–354.

Magurran, A.E. and Henderson, P.A. 2010. Temporal turnover and the maintenance of diversity in ecological assemblages. Philosophical Transactions of the Royal Society B-Biological Sciences 365, 3611–3620.

Margules, C. and R. Pressey. 2000. Systematic conservation planning. Nature 405, 243–253.

Mason, N.W.H., de Bello, F., Dolezal, J. and Leps. J. 2011. Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. Journal of Ecology 99, 788–796.

McCraacken, D.I. 2009. Machair invertebrates: the importance of mosaicness. Glasgow Naturalist. 25 (supplement) pp. 29-30.

McGill, B.J., Maurer, B.A. and Weiser, M.D. 2006. Empirical evaluation of neutral theory. Ecology 87, 1411-1423.

McGill, B. J. 2010. Towards a unification of unified theories of biodiversity. Ecology Letters 13, 627–642.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: current state and trends. Island Press, Washington, DC.

Mokany, K., Ash. J. and Roxburgh. S. 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. Journal of Ecology 96, 884–893.

O'Briain, M. 2005. EU biodiversity policy context for the conservation of estuaries and dunes. In: Herrier, J.L., Mees, J., Salman, A., Seys, J., van Nieuwenhuyse, H. and Dobbelaere, I. (eds) Dunes and Estuaries 2005 proceedings. pp. 7-12. International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium, 2005. VLIZ Special Publication 19. Flanders Marine Institute (VLIZ), Oostende, BE.

Osgathorpe, L.M., Park, K., Goulson, D., Acs, S. and Hanley, N. 2011. The trade-off between agriculture and biodiversity in marginal areas: can crofting and bumblebee conservation be reconciled. Ecological Economics 70, 1162-1169.

Ovington, J. 1950. The afforestation of the Culbin Sands. Journal of Ecology 38, 303–319.

Owen, N.W., Kent, M. and Dale, P. 1996. The Machair vegetation of the Outer Hebrides: a review. In Gilberson, D., Kent, M. and Gratton, J. (eds), The Outer Hebrides: the last 14000 years. Sheffield University Press, Sheffield. pp. 123-131.

Owen, N.W., Kent, M. and Dale, P. 2000. Ecological effects of cultivation on the Machair sand dune systems of the Outer Hebrides, Scotland. Journal of Coastal Conservation 6, 155-170.

Owen, N.W., Kent, M., Dale, P. and Wilson, J. 2004. Plant species and community responses to sand burial on the machair of the Outer Hebrides. Journal of Vegetation Science 15, 669-678.

Pakeman, R.J., Huband, S., Kriel, A. and Lewis, R.J. 2011. Changes in the Management of Scottish Machair Communities and Associated Habitats from the 1970s to the Present. Scottish Geographical Journal 127, 267-287.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37, 637–669.

Parmesan, C. Ryrholm, N., Stefanescus, C., Hill, J.K., Thomas, C.D. et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399, 579-583.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M. et al. 2012. Recent plant diversity changes on Europe's mountain summits. Science 336, 353–355.

Redpath, N., Osgathorpe, L.M., Park, K. and Goulson, D. 2010. Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland. Biological Conservation 143, 492-500.

Rejmánek, M. and Rosén, E. 1992. Influence of colonizing shrubs on species-area relationships in alvar plant communities. Journal of Vegetation Science 3, 625-630.

Ritchie, W. 1976. The meaning and definition of machair. Transactions of the Botanical Society of Edinburgh 42, 431-440.

Root, T., Price, J., Hall, K., Schneider, S., Rosenzweig, C. and Pounds, J. 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfied, J., et al. 2000. Biodiversity – global biodiversity scenarios for the year 2100. Science 287, 1770-1774.

Shaw, M.W., Hewett, D.G. and Pizzey, J.M. 1983. Scottish coastal survey. Institute of Terrestrial Ecology. Bangor Research Station, Bangor, Gwynedd.

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C. and Firbank, L.G. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. Proceedings of the Royal Society B 273, 2659-2665.

Sotherton, N.W. 1998. Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. Biological Conservation 83, 259–268.

Suding, K.N., Gross, K.L. and Houseman, G.R. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19, 46-53.

Thomas, J., Telfer, M., Roy, D., Preston, C., Greenwood, J. et al. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303, 1879–1881.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. and Prentice. I.C. 2005. Climate change threats to plant diversity in Europe. Proceedings of The National Academy of Sciences 102, 8245-8250.

van der Maarel, E. and Usher, M.B. 1997. Recreational use of dry coastal ecosystems. In: van der Maarel, E. (eds) Dry coastal ecosystems 2C: general aspects. pp.519-529. Elsevier, Amsterdam, NL.

Wallace, A.R. 1870. Contribution to the theory of natural selection. Macmillan. London.

Walther, G.R., Berger, S. and Sykes, M.T. 2005. An ecological "footprint" of climate change. Proceedings of the Royal Society B-Biological Sciences 272, 1427–1432.

Welch, R.C. 1989. Invertebrates of Scottish sand dunes. Proceedings of the Royal Society of Edinburgh. Section B-Biological Sciences 96, 267-287.

Westhoff, V. 1989. Dunes and dune management along the North Sea coasts. In: van der Meulen, F., Jungerius, P.D. and Visser, J. (eds.) Perspectives in coastal dune management. pp. 44–51. Proceedings of the European Symposium Leiden, September 7–11, 1987, The Netherlands. SPB Academic Publishing, The Hague, NL.

Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? Trends in Ecology and Evolution 12, 266–269.

Chapter Two

Identifying the multi-scale spatial structure of plant community determinants on a national scale

ABSTRACT

The significance of climate and land use management as determinants of plant species composition of Scotland's soft coasts is assessed. This Chapter investigates how these determinants are spatially scaled, and uses the results to examine the relative contribution of different community assembly processes in governing the coastal plant communities of a national resource.

National-scale survey data of Scotland's soft coasts, and a subset representative of Machair grassland, a conservation priority habitat is used. Principal Coordinates of Neighbour Matrices (PCNM), an eigenvector based method, was used to assess the spatial component of environmental determinants at multiple scales. The variation partitioning framework was applied to unravel the scale-specific importance, relative to the study design (Broad > 50km, Meso 10-50km & small+fine 1.5-10km) of each environmental predictor set.

Modelled environmental and spatial predictors captured approximately 20% of the variation for both response matrices. Management predictors captured significant proportions, identifying vegetation structure, proxies for grazing intensity and disturbance to be important descriptors of patterns in species composition for both datasets. The spatial scale of management predictors was poorly captured by modelled PCNM variables, suggesting spatially dependent management variables operate at finer spatial scales than this study could detect. Climate also captured significant, yet smaller fractions of variation compared to management. Potential evapo-transpiration (PET) and humidity were identified as important climatic determinants of species composition operating entirely at the broad spatial scale. Pure spatial fractions across all scales were significant ($p \leq 0.001$) for both datasets alluding to unmeasured spatially-structured environmental variables such as soil chemistry and/or exposure at the larger scales, and potentially biotic process such as seed dispersal at the finest-scale.

The use of spatial PCNM variables within the variation partitioning framework is a valuable tool for dissecting the scale-specific importance of environmental determinants of species composition. Results from this study reveal important climatic and management determinants of Scotland's soft coast and Machair vegetation, and help identify the relative scale at which they operate, suggesting these communities to be maintained primarily through niche processes at broad-spatial scales. The spatial resolution of this study prevented analyses from identifying whether niche processes operate to a similar extent at finer scales, or if biotic processes dominate.

2.1 Introduction

Beta diversity, the variability in species composition from place to place (Whittaker 1960, 1972; Legendre et al. 2005), has been recognised as having a pivotal role in identifying and understanding diversity patterns at multiple scales (Soinenen et al. 2007). Mechanisms responsible for driving β-diversity can be seen as either deterministic or stochastic processes; understanding the relative contributions of these drivers is a continuing challenge for ecologists (Barot and Gignoux 2004; Laliberté et al. 2009) and remains at the focal point of the niche (Hutchinson 1957) and neutral (Hubbell 2001) theories of plant species assembly.

It has been suggested that environmental heterogeneity has a high influence in structuring assemblages at broader spatial scales, while stochastic processes such as dispersal tend to operate at finer spatial scales (Legendre 1993; Laliberté et al. 2009; Gazol and Ibañez 2010a). With this in mind, the processes controlling β-diversity cannot be mutually exclusive. In fact it is more likely that drivers contribute differently depending on the spatial scale under study (Laliberté et al. 2009; Gazol and Ibañez 2010a). Consequently, much research is now focused on the investigation of spatial structure to aid in the interpretation of patterns of diversity (Wiens et al. 1986, Levin 1992; Borcard and Legendre 1994, 2002).

However, incorporating spatial variation into ecological models requires a statistical tool capable of describing spatial relationships among ecological data as model predictors or covariates (Dray et al. 2006). This has been achieved with success through using Principal Coordinates of Neighbour Matrices (PCNM; *for details see* Borcard and Legendre 2002; Borcard et al. 2004), for several ecological applications (Borcard et al. 2004; Legendre et al. 2005; Carvalho et al. 2011) and can be used to dissect the spatial variability of species community data at multiple spatial scales. This means that the scale-specific contribution of environmental heterogeneity and other spatial processes governing β-diversity can be quantified (Laliberté et al. 2009; Gazol and Ibañez 2010a). This approach is new but studies have revealed (i) the influence of environmental filters on species community composition, (ii) the scale of environmental heterogeneity, (iii) the influence of unmeasured variables, and/or (iv) the effect of biotic processes such as seed dispersal (Pottier et al. 2009; Gazol and Ibañez 2010a,b, Hernandez-Stefanoni et al. 2011).

In this Chapter PCNM and a variation partitioning framework are used to investigate the spatial variability among coastal plant species assemblages of almost an entire national resource; the soft coast areas of Scotland, UK. These areas typically include sand dune habitats, but particularly on the far western seaboard of Scotland also include the globally-rare biotype, termed 'Machair', globally confined to Scotland (30,000 ha) and Ireland (10,000 ha; Anon. 2008).

Alongside climate the main driver of vegetation patterns in dune systems is succession from seaward embryo dunes to landward moorland or scrub. However, among these transient habitats, vegetation patterns, particularly those for coastal and Machair grasslands are also closely linked to forms of low-intensity disturbance through management for arable agriculture or grazing (livestock based but with associated rabbit grazing). In regions that support Machair, rotational agricultural practices can result in a highly heterogeneous landscape behind the dune ridge, significantly influencing the vegetation of these habitats.

Within Europe, the area of coastal dune vegetation has declined by about one-third since the late 1970s (O'Briain 2005), principally through agriculture, recreation and development. Furthermore, socio-economic change has seen a substantial shift in the way the Machair and Machair grasslands are managed, threatening both their biodiversity and cultural heritage value (Pakeman et al. 2011). In addition, there is the continued threat of coastal erosion of these habitats, exacerbated by sea level rise, which, along with other impacts of climate change, results in coastal dune systems being categorised among the most vulnerable ecosystems in Europe. Therefore, the identification of important environmental determinants that govern the vegetation composition of these habitats is important from a local-, regional- and continental-wide conservation management perspective, as variables which are important drivers of vegetation at local scales are likely to differ from those that are important at landscape or global scales (Corney et al. 2006).

First, using an extant dataset of species composition across Scotland's soft coasts the variation partitioning framework was applied to assess the relative importance of climate, management and local environmental drivers of β-diversity. Second, their scale-specific contributions are assessed through quantifying spatial processes using PCNM. It is expected for climatic correlates to be broadly spatially structured, while land use operates at much smaller scales relative to the national-scale of this study. This study tests the hypothesis that environmental heterogeneity has greater influence on the vegetation composition on a national-scale, but does not preclude the operation of smaller scale neutral or biotic processes.

2.2 Materials and Methods

2.2.1 Study area

The vegetation of Scotland's soft coast sites and its associated landforms were used as a case study. Their extent in Scotland alone is ca. 50,000 ha, of which roughly one third is classified as Machair grassland (Dargie 2000). Confined to the western and northern reaches of Scotland, the Machair ecosystem is a distinct and bio-diverse coastal bio-type that includes all transient habitats from seaward embryo dunes to inland sand-affected peatlands, including low-lying, species-rich grasslands listed on Annex I of the EC Habitats and Species Directive (Council Directive 92/43/EEC). Its distinctiveness derives from a combination of a calcareous substrate (shell sand), a hyper-oceanic climate and relatively extensive agricultural practices. East coast systems are generally based on more acidic substrates, consist mainly of bay dunes, spit dunes and ness dunes, and have a less oceanic climate than those on the west coast.

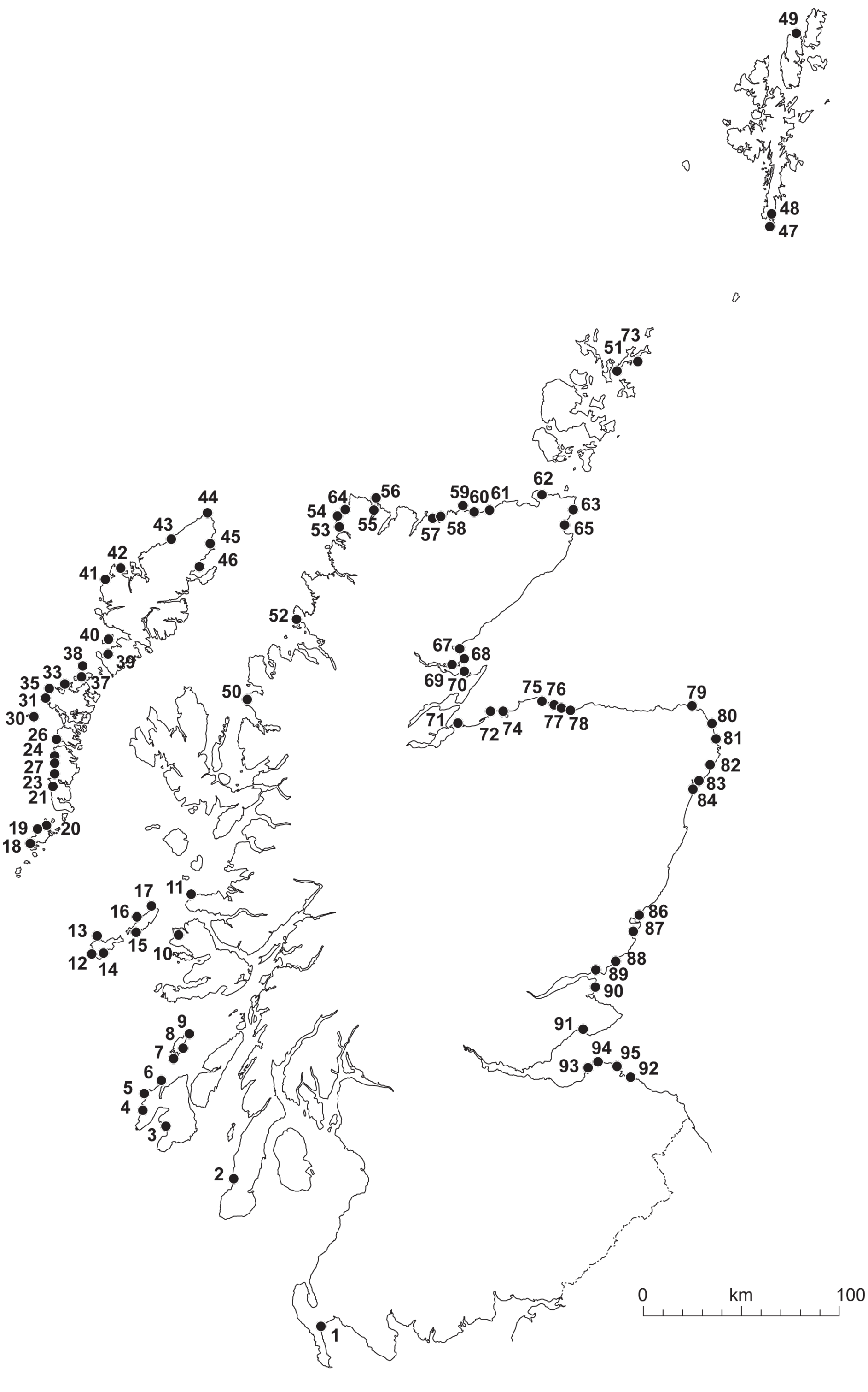


Fig. 2.1 Distribution of soft coast sites sampled around Scotland's coast. For detailed site information see Appendix 2.1

2.2.2 Vegetation sampling

The vegetation survey was carried out between June and September 1975 to 1977 as part of the Scottish Coastal Survey (Shaw et al. 1983). Estimates of cover (minimum 1%) were made for all vascular plant species within a series of nested quadrats, from 1 m^2 to 14.1 m^2. Described as an additive sampling procedure (Bunce and Shaw 1973), only records from the 5 m x 5 m quadrat were used (hereafter referred to as plot), of 3,847 plots. Ground cover, bryophytes and lichens were also measured. For a detailed description of the methodology of the Scottish coastal survey see Shaw et al. (1983), for study site locations see Figure 2.1.

Nomenclature follows Kent (1992), and old nomenclature was updated to current taxonomy. Closely related species, which are difficult to separate consistently, were combined at the genus level, i.e. *Euphrasia, Hieracium* and *Taraxacum* species. Bryophytes and lichens were given a collective abundance value and were not analysed at genus or species level, but rather as a single unit of percentage occurrence.

2.2.3 Environmental and Management Variables

A number of environmental variables were measured in each plot (Table 2.1). Past and present land use and measures of current management regimes were recorded. Plots were classified into one of four land use categories (cultivated, recent-cultivation, old-cultivation or no-cultivation). Measures of current grazing activity scaled 0-3 (0 = no grazing; 1 = light; 2= moderate; 3= heavy), and presence and absence of grazers, i.e. rabbits, deer, sheep and cattle, were noted. Total cover of grasses, forbs, shrubs and trees were measured as three vegetation height classes (<20cm, 20cm – 50cm & > 50cm) for grasses and forbs, and (0.5-2.0m & >2.0m) for shrubs and trees. Cover was scored from 0-3; zero being absent and three representing total cover.

In addition, a suite of long-term average climatic variables were derived from the UK Meteorological Office 5 km monthly gridded dataset, UKCP09, (Perry and Hollis 2005; Table 2.1), calculated using data from 1960–1977. For sites requiring interpolation, a weighted average of its neighbours (i.e. neighbouring 5km grid cells) was taken; temperature variables were adjusted by a lapse rate of 0.6°C/100 m, using altitudinal data derived from 1km detailed digital terrain models. Furthermore, four climate indices were calculated, describing the climate as a linear function of combined climatic parameters. These included relative measures of Oceanicity (*days > 1mm precipitation/temperature range*), Potential Evapotranspiration (PET, Hagreaves and Samani, 1985), an Aridity index (Thornthwaite 1948) and Growing Degree Units (GDU; *number of days of the year above 6.0°*C).

Table 2.1 Description of environmental predictors derived for sites surveyed in the Scottish soft coast survey; number and type of variables used in the analysis and their abbreviations are presented. V refers to variable type: b. binary; c. continuous; f. factorial; o. ordinal. N refers to the number of variables per group.

Predictor set	Variable group	V	N	Description	Variables	Abbreviation
Climate	Climate	c	14	UK Met Office 5km monthly gridded climatic data and climatic indices. Long-term averages 1961-1977.	Minimum winter temperature (°C)	MinWT
					Maximum summer temperature (°C)	MaxST
					Sun duration (hrs-1day)	SD
					Cloud cover ($\%^{avgpcm}$)	CC
					Total precipitation (mm)	TP
					Days of precipitation >1mm	DsP1
					Days of precipitation >10mm	DsP10
					Days of ground frost (d^{-1year})	GndFst
					Days of snow cover (d^{-1year})	Snow
					Humidity ($\%^{avgpcm}$)	Hum
					Potential evapotranspiration (mmd^{-1})	PET
					Aridity	Arid
					Oceanicity	Ocnty
					Growing degree units ($^{GDU's}$)	GDU
Management	Animal signs	b	5	Plot level presence/absence of dung from 5 herbivore species	Cattle	N/A
					Sheep	N/A
					Rabbits	N/A
					Deer	N/A
					Horse	N/A
	Grazing pressure	f	4	Intensity of herbivore grazing	None	NoGrz
					Light	LghtGrz
					Moderate	ModGrz
					Heavy	HvyGrz
	Vegetation structure	o	6	Indication of vegetation height for each plot (0,1,2,3 = no, sparse, moderate and full cover respectively) for three height categories for grasses and higher plants. Shrubs and trees are scaled differently.	< 20cm	Struc<20cm
					20-50cm	Struc 20-50cm
					> 50cnm	Struc>50cm
					Shrubs 0.5-2m	Shrb_0.5-2m
					Shrubs > 2m	Shrb>2m
					Trees less than 5m	Tree
	Cultivation	f	4	Plot level presence/absence of different cultivation states, from no cultivation to current standing crop	No Cultivation	NoCult
					Standing Crop	StdCrp
					Recent Cultivation (≤ 3 years)	RecCult
					Old Cultivation (> 4 years)	OldCult
Local Environment	Distance to sea	c	2	A measure of the shortest distance per plot from the mean spring high water mark	Distance to the sea (m)	Dis2Sea

2.2.4 Statistical analysis

2.2.4.1 Species~Environment interactions

Species abundance data were collated into two response matrices. Those encompassing the full study area, representative of almost an entire resource of Scotland's soft coast sites (Y^f), and a sub-set selected to best represent areas of Machair grassland (Y^s). The latter was achieved by allocating all samples to the National Vegetation Classification (NVC; Rodwell 1991a, 1991b, 1992, 2000) using the software package 'TABLEFIT' (Hill 1993). Sites allocated a NVC typical of Machair grassland as defined by Angus (2006) were included in this subset dataset (Table 2.2).

The presence of many rare species increases noise within a dataset. Therefore prior to analyses; species data matrices were constrained by removing species that were present in less than 0.025% of the total number of plots. Species present in less than 10 plots (matrix Y^f; n = 3605) and less than 4 plots (matrix Y^s; n = 1200) were removed. This considerably reduced the number of species included for analysis; matrix Y^f reduced from 496 to 311 species and matrix Y^s reduced from 257 to 210 species. The number of plots remained unchanged i.e. 3605 and 1200 respectively. The resulting matrix was transformed using the Hellinger transformation that expresses the abundance as a fraction of the sum of the abundances of all species in each plot and takes the square root. This procedure deals with the "species abundance paradox", where the Euclidean distance between two sites that share zero species is found to be smaller than distances between sites sharing two or more species (Legendre and Gallagher 2001).

Table 2.2 Vegetation classification of Machair habitats, as defined by Angus (2006).

NVC	Vegetation description
SD8a	*Festuca rubra - Galium verum* fixed dune grassland
SD8c	*Festuca rubra - Galium verum* fixed dune grassland
SD8d	*Festuca rubra - Galium verum* fixed dune grassland
SD8e	*Festuca rubra - Galium verum* fixed dune grassland
MG11	Inundation grassland – *Festuca rubra*
SD17	*Potentilla anserina - Carex nigra* dune slack

2.2.4.2 Spatial modelling

PCNM analysis was applied to generate spatial eigenvectors for use as spatial predictors in multivariate regression (Dray et al. 2006). Eigenvectors generated through PCNM analysis have the advantage of being completely orthogonal to one another, allowing them to be used in additive, scale-specific models (Borcard and Legendre 2002; Borcard et al. 2004). Furthermore, they are representative of the complete spectrum of spatial scales encompassed by the sampling design (Borcard and Legendre 2002), and thus potentially mirror various spatially scaled ecological processes measured or unmeasured. The PCNM methodology builds a spatial matrix **W** based on the spectral decomposition of spatial relationships among the sampling sites (Borcard et al. 2004). Variables from this matrix can then be used as predictors to quantify the spatial dependence of the response matrices **Y**. The PCNM procedure is described in detail by Dray et al. (2006), but in summary, essentially involves the following three steps (Borcard and Legendre 2002).

(i) Calculate a pairwise geographic (Euclidean) distance matrix (**D** = [d_{ij}] between n sites.

(ii) Build a truncated connectivity matrix (**W** = [w_{ij}]). When $d_{ij} < t$ $w_{ij} = [1-(d_{ij}/4t)^2]$ (Where t is the user defined truncation distance. Commonly selected to be the minimum distance that keeps all sites connected, as defined by the minimum spanning tree algorithm).

(iii) Compute the eigenvalues and eigenvectors of the centred matrix **W** through principal coordinate analysis.

Truncation leads to the retention of only the closest neighbours, but also results in the generation of negative eigenvalues. Therefore, only the principal coordinates associated with positive eigenvalues were selected for use as spatial descriptors (here after referred to as PCNM variables). For the full response matrix Y^f (n=3605, t=96.31km) 312 PCNM variables with eigenvectors corresponding to positive eigenvalues were obtained. This compared with 87 PCNM variables for the subset response matrix Y^s (n=1200, t=112.29km) representative of Machair grassland vegetation. Calculations of the principal coordinate variables were performed with the SpacemakeR package of S.Dray (<http://pbil.univ-lyon1.fr/members/dray/software.php>), within the R language environment (R Development Core Team 2012).

2.2.4.3 Multi-scale spatial predictors

PCNM variables were used to detect multi-scale spatial structures of environmental predictors. Forward selection of all PCNM variables for the full (Y^f; n=312), and subset (Y^s; n=87) matrices was carried out following the procedure of Blanchet et al. (2008) with α restricted to 0.10 to ensure a manageable number of selected variables. Community composition data were detrended, (i.e. remove broad-scale linear trends) for both response matrices Y^f and Y^s. This is an important process prior to analysis, as although PCNM is capable of recovering linear trends, in doing so this may obscure finer-scale spatial structures being recovered (Borcard and Legendre 2004). This in turn limits the number of PCNM variables in the spatial matrix **W.** The selection process fitted 30 (Y^f) and 20 (Y^s) significant positive PCNM variables tested by Moran's I (Borcard et al. 2004; Table 2.3).

Selected PCNM variables were grouped by variogram analysis (Wagner 2003) into sub-model predictor sets based on their spatial autocorrelation range (SAC). The SAC of each PCNM variable was calculated through multiple semi-variograms using the 'variofit' function of the R package 'geoR' (Ribeiro and Diggle 2001). The autocorrelation range of selected PCNM variables are shown in Fig. S2.1 (*see Supplementary material*). Table 2.3 presents the scaled PCNM variables showing the

SAC range for both response matrices. It is important to note that the scales here termed broad, meso, small and fine-scales are relative only to the study in question and defined by the spatial grain (resolution) and spatial lag (distance among plots) of the sampling procedure (Laliberté et al. 2009); any processes finer than the spatial grain or greater than the spatial lag will not be detected.

Table 2.3 Model-selected PCNM variables following forward selection (α = 0.10) for both the full (Y^f) and the Machair subset (Y^s) datasets. Variables are grouped according to their spatial autocorrelation (SAC) range assessed through individual variogram analysis.

Spatial Scale	Full Scottish soft coast data (Y^f)		Subset Machair data (Y^s)	
	PCNM number	SAC range (km)	PCNM number	SAC range (km)
Broad (≥50km)	1	153.5	2	140.5
	2	94.5	4	105.5
	3	130.5	1	94.5
	4	100.5	3	87.5
	5	64.5	9	65.5
	6	70.5		
	7	73.5		
	8	90.5		
	9	83.5		
	10	176.5		
	138	87.5		
Meso (≥10km & <50km)	11	15.5	6	35.5
	13	14.5	5	23.5
	14	22.5	7	15.5
	16	12.5	10	14.5
	17	12.5	8	13.5
	18	14.5		
	21	15.5		
Small (≥2km & <10km)	12	5.5	11	8.5
	15	3.5	12	8.5
	19	7.5	14	8.5
	20	8.5	19	8.5
	23	2.5	13	6.5
	26	4.5	15	6.5
	28	2.5	16	5.5
	29	3.5	83	5.5
	31	4.5		
	34	6.5		
	253	9.5		
Fine (<2km)	53	1.5	22	2.5
			35	1.5

2.2.4.4 Model selection and variation partitioning

Variation partitioning (designed to quantify the variation in community composition that is uniquely attributable to one set of environmental variables, after controlling for the effects of another set (Borcard et al. 1992)), was used to assess the relative fractions of variation in species composition of Scotland's soft coast and Machair habitats in terms of variation explained by environmental and spatial variables. The environmental matrix was subdivided into three predictor sets representing predictors of climate, management and local environment (Table 2.1). Stepwise selection was used to identify the variables within each environmental predictor set that were significantly associated with species composition ($p < 0.01$). Variable inflation factors (VIF) identified variables with highly co-linear constraints. These variables were subsequently removed from analysis (ter Braak and Šmilauer 2002; Table 2.4).

Variation partitioning was performed through calculating a series of partial and non-partial Redundancy Analyses. This procedure allows the user to determine independent and shared fractions between modelled environmental and spatial predictors. To investigate how environmental predictor sets are scaled, the response matrices Y^f and Y^s were analysed further in relation to three spatial models of scaled PCNM variables. The process of variation partitioning was repeated, exchanging the whole set of spatial predictors with subsets representative of broad, meso and combined small and fine spatially scaled PCNM variables. The significance of testable fractions was assessed through 9999 unrestricted permutations. Variation partitioning analyses were carried out using the "vegan" package (Oksanen et al. 2007), within the R language environment (R Development Core Team 2012).

2.3 Results

2.3.1 Model selection

Results from the forward selection processes found all climatic variables to significantly explain variation in species composition ($p < 0.001$) for both responses matrices, i.e. the full dataset (Y^f) and the Machair subset (Y^s). However, some variables displayed high co-linearity and were subsequently removed from the final models (Table 2.4). Potential evapotranspiration (Y^f), humidity (Y^s) and predictors of vegetation structure (Y^f & Y^s) were identified to best explain patterns of variation among species composition of Scotland's soft coast and Machair habitats (Table 2.4).

2.3.2 Variation partitioning

Environmental and spatial predictors explained 20% (Y^f) and 21% (Y^s) of the total variation in species composition between sites. Variation partitioning showed predictor sets management and space to explain relatively equal proportions of the variation among (Y^f), accounting individually for circa 11% of the total variation (Fig. 2.2i). Climate explained 7.5% of the variation, whereas local environment explained 2%. Variation partitioning of the Machair data found management to explain the greatest amount of variation in species composition (11%), followed by space (9%), climate (8%) and local environment (2%; Fig. 2.3i).

Table 2.4 Selected significant explanatory variables derived from the Scottish soft coast survey using Redundancy Analysis (Full data, $\mathbf{Y}^f$) and (Machair subset, $\mathbf{Y}^s$); **VIF**: Variance Inflation Factor.

Environmental predictor set	**Variable**	**Full data**		**Subset (Machair)**	
		Pseudo-F	***VIF***	***Pseudo-F***	***VIF***
Climate	PET 61-77Avg	129.2*	17.23	8.72*	16.26
	Oceanicity 61-77Avg	33.55*	18.70	3.04*	←*c*
	Days Snow lying	22.42*	3.32	4.19*	3.84
	Days Ground Frost	16.30*	6.90	4.69*	5.58
	Max July Temperature (°C)	17.88*	←*c*	4.65*	18.39
	Sun Duration	17.45*	6.52	4.77*	16.35
	Min Jan Temperature (°C)	18.38*	←*c*	15.80*	←*c*
	Cloud Cover	11.43*	5.17	3.99*	12.59
	Days Precipitation > 10mm	11.06*	16.92	8.13*	10.93
	Days Precipitation > 1mm	10.28*	8.18	10.37*	5.39
	GDU	9.96*	5.17	15.35*	10.78
	Humidity	8.05*	8.09	29.57*	9.63
	Aridity 61-77Avg	7.26*	19.39	5.99*	10.93
	Total precipitation (mm)	10.07*	←*c*	9.09*	13.26
		Pseudo-F	***VIF***	***Pseudo-F***	***VIF***
Management	Vegetation structure <20cm	133.2*	1.43	12.32*	1.17
	Vegetation structure 20-50cm	65.90*	1.30	62.97*	1.24
	Shrub 0.5-2m	47.17*	1.08	N/A	N/A
	Rabbit	33.57*	1.27	7.96*	1.08
	Cattle	29.78*	1.26		
	Vegetation structure >50cm	23.46*	1.32	28.05*	1.33
	Grazing Score	8.80*	1.95-2.52	7.50*	1.43-1.86
	Cultivation Factor	7.51*	1.00-1.03	5.08*	1.02-1.04
	Tree	13.47*	1.06	N/A	N/A
	Sheep	10.46*	1.21		
	Shrub >2.5m	4.03	-	N/A	N/A
	Deer	3.03	-		
	Horse	1.26	-		
		Pseudo-F	***VIF***	***Pseudo-F***	***VIF***
Local Environment	Distance from Sea (m)	57.51*	-	22.15*	-

Variables denoted with a ←c refer to highly collinear variables and were subsequently dropped from the model.

[*] $p \leq 0.01$. Significance of each model against 9999 permutations (unrestricted (Climate & Local environment), stratified within site (Management)). N/A: For analyses of the subset data the variables Tree, Shrub 0.5-2 m & Shrub >2.5 m were dropped as their means were equal to zero.

Partial RDA revealed independent fractions of variation, identifying management (*fraction a,* Figs. 2.2i & 2.3i) to independently explain 6.2% (Y^f) and 7.2% (Y^s) of the variation in species composition. The independent fractions explained by climate, local environment and space accounted for 1.4%, 1.1% and 3.9% (Y^f) and 2.5%, 0.9% and 3.6% (Y^s). Of the fraction explained by the spatial PCNM variables, 64% (Y^f) and 60% (Y^s) was attributable to broad-scale spatial structures. Meso-scale PCNM variables accounted for approximately 20% (Y^f) and 21.5% (Y^s), while the remaining fractions represented small to finer-scaled spatial structures (Figures 2.2ii and 2.3ii).

Shared fractions among the response matrix (Y^f) revealed climate to be largely spatially structured, (3.0%, *fractions [i]*, Fig. 2.2i), of which it's shared fraction with management (2.2%, *fraction [k]*) was also entirely spatially structured. Management also revealed a degree of spatial structuring independent of that shared with climate (1.4%, *fraction [h]*). Similarly, shared fractions among the response matrix (Y^s) also revealed climate to be spatially structured, (3.0%, *fraction [i],* Fig. 2.3i). Shared fractions between climate and management were partitioned between that showing spatial dependence (1.7%, *fraction [k]*), and that independent of space (0.5%, *fraction [e]*). Management also revealed a degree of spatial structuring independent of that shared with climate (1.0%, *fraction [h]*).

Local environment showed no spatial dependence and very little shared variation with other environmental predictor sets. The residual fraction that remained unexplained was approximately 80% (Y^f; Fig. 2.2i) and 81% (Y^s; Fig. 2.3i).

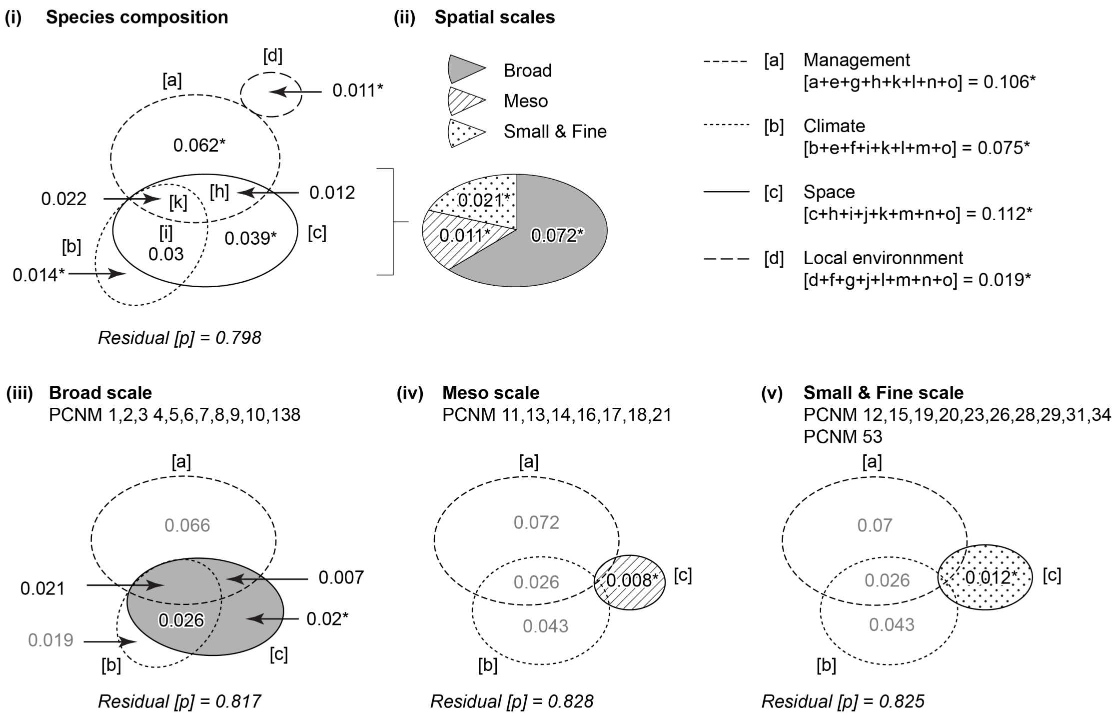


Fig. 2.2 **(i)** Variation partitioning of the full Scottish soft coast data (**Y**^{f}). **(ii)** Variation partitioning of the spatial fraction "c" into relative scales (broad, meso and small+fine)*. **(iii-v)** Variation partitioning where space represents either broad- **(iii)**, meso- **(iv)** or small + fine **(v)** scaled PCNM vectors.
Greyed values represent over estimated fractions, as not all spatial predictors are included in each model. Spatial predictors failed to represent the spatial structuring of the local environmental variable 'distance to sea', and thus are not displayed in the variance partitioning plots iii-v. *Orthogonal PCNM eigenvectors present zero covariance and so are presented additively.

2.3.3 Multi-scale spatial component

Variation partitioning was repeated to represent space as broad-, meso- and small + fine-scaled spatial PCNM variables (Fig. 2.2 iii-v and Fig. 2.3 iii-v). All independent spatial fractions of scale-specific models were statistically significant ($p \leq 0.001$).

Of the variation explained by broad-scale PCNM variables (Figs. 2.2ii & 2.3ii), shared fractions were almost entirely represented by climatic, Y^f = 36% and Y^s = 42%, with the fraction shared by both climate, management and space accounting for 29% (Y^f) and 25% (Y^s) respectively (Figs. 2iii & 3iii). Fractions explained by management accounted for 10% (Y^f) 7% (Y^s). The independent fraction unexplained by either of the environmental predictor sets, accounted for 2.0% (Y^f) and 1.8% (Y^s) of the variation in species community composition (Figs. 2iii & 3iii). Species composition was revealed to have significant spatially-dependent fractions at all spatial scales (Y^f; Figs. 2.2iv-v) and (Y^s; Figs. 2.3iv-v), however only for response matrix (Y^s) did either of the environmental predictor sets reveal spatial structuring at scales less than 50km, exhibiting a small fraction of variation explained by management between 1.5 – 10km (Fig. 2.3v).

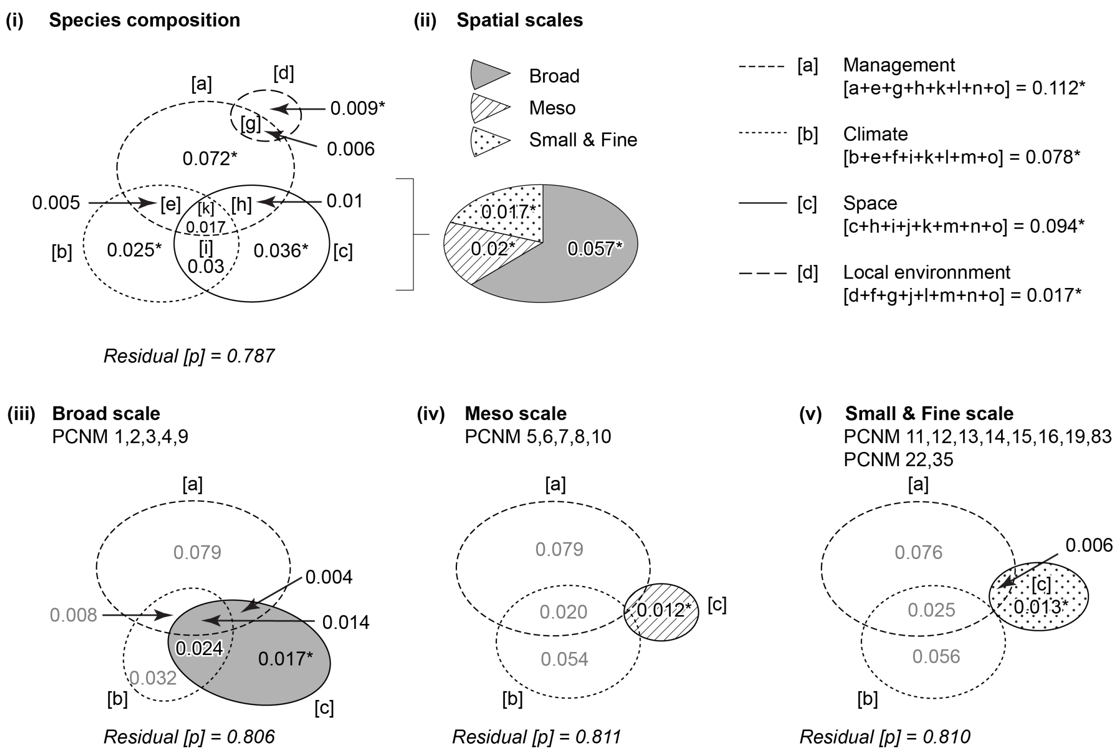


Fig. 2.3 (i) Variation partitioning of the subset Machair dataset (**Y^s**). **(ii)** Variation partitioning of the spatial fraction "c" into relative scales (broad, meso and small+fine)*. **(iii-v)** Variation partitioning where space represents either broad- **(iii)**, meso- **(iv)** or small + fine **(v)** scaled PCNM vectors.
Greyed values represent over estimated fractions, as not all spatial predictors are included in each model. Spatial predictors failed to represent the spatial structuring of the local environmental variable 'distance to sea', and thus are not displayed in the variance partitioning plots iii-v. *Orthogonal PCNM eigenvectors present zero covariance and so are presented additively.

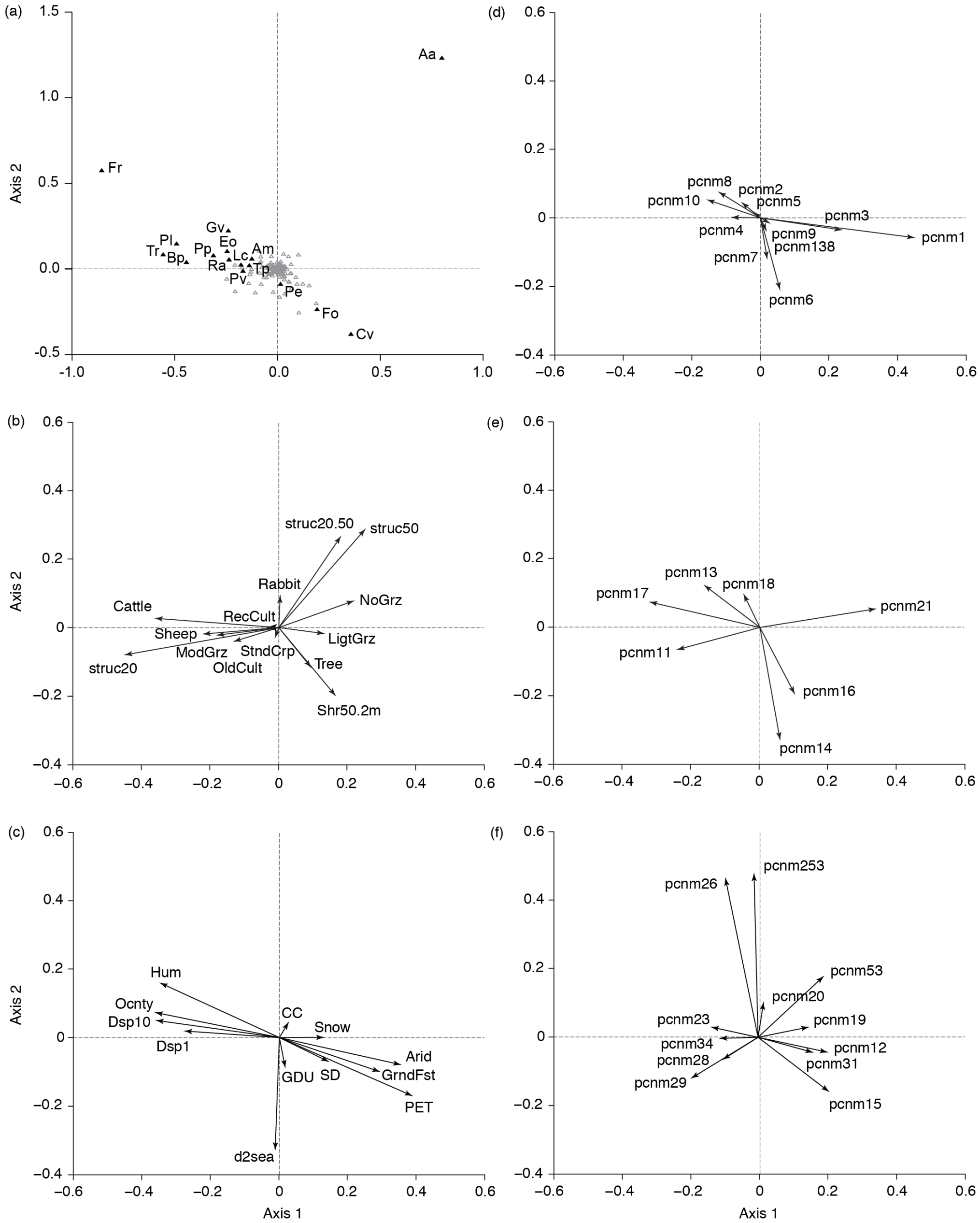


Fig. 2.4 Redundancy analysis (RDA) plots of species composition of all plots (n= 3605) surveyed across Scotland's soft coasts, constrained by all selected environmental and spatial determinants identified by stepwise selection. a) Each symbol represents one species, displayed in bold are those species which displayed a significant statistical relationship ($p < 0.001$) and a goodness of fit ($r^2 \geq 0.10$ along Axis 1 and/or Axis 2. Species are represented by the following letter codes: Aa *Ammophila arenaria,* Am *Achillea millefolium*, Bp *Bellis perenis*, Cv *Calluna vulgaris*, Eo *Euphrasia officinalis*, Fo *Festuca ovina*, Fr *Festuca rubra*, Gv *Galium verum*, Lc *Lotus corniculatus*, Pl *Plantago lanceolata*, Pp *Poa pratensis*, Pv *Pruna vulgaris*, Ra *Ranuculus acris*, Tp *Trifolium pratense,* Tr *Trifolium repens*. b) Management determinants. c) Climatic and local environmental determinants. d) Broad-scale spatial determinants. e) Meso-scale spatial determinants. f) Small+Fine-scale spatial determinants.

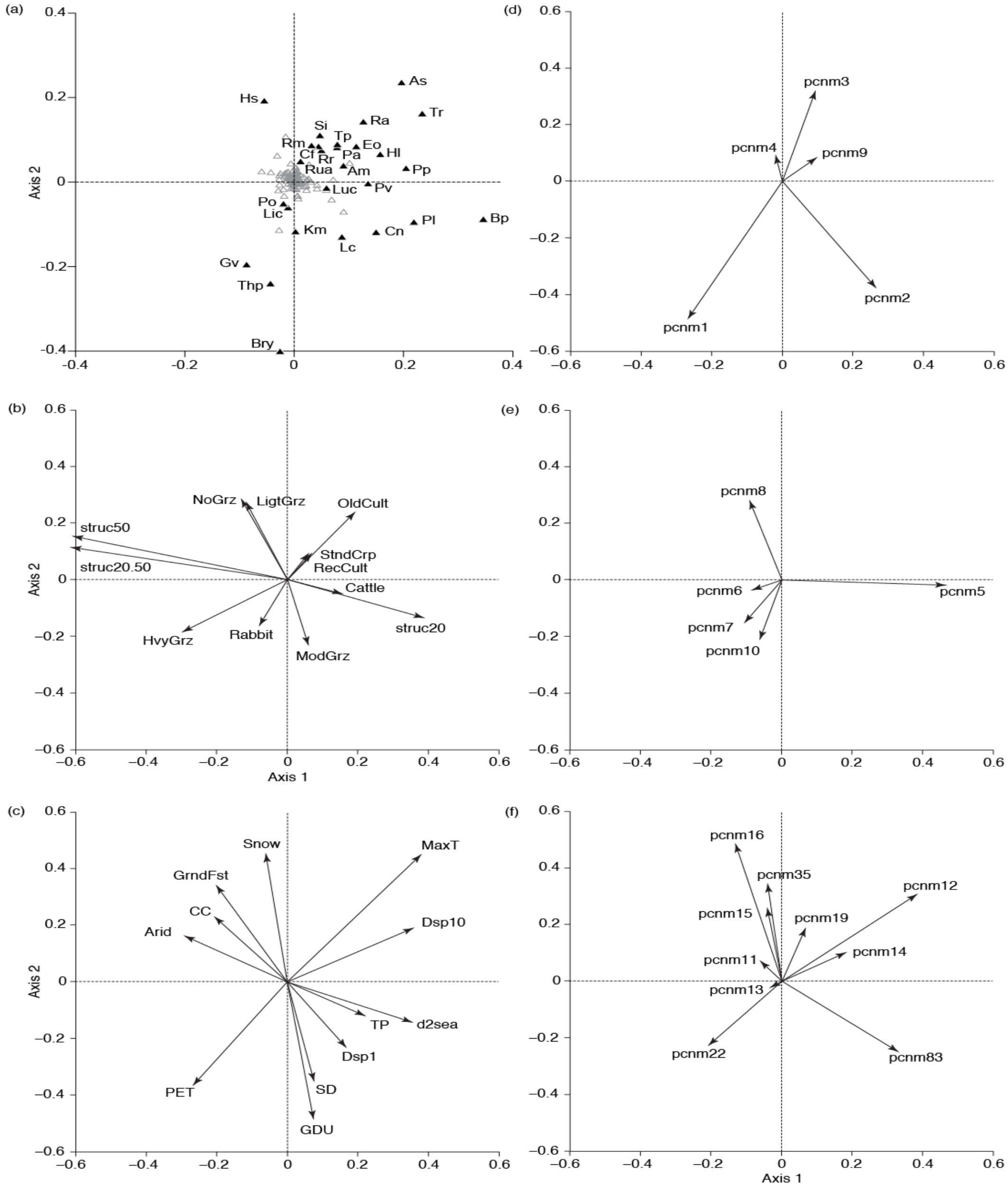


Fig. 2.5 Redundancy analysis (RDA) plots of species composition of Machair plots (n= 1200) surveyed across Scotland's soft coasts, constrained by all selected environmental and spatial determinants identified by stepwise selection. a) Each symbol represents one species, displayed in bold are those species which displayed a significant statistical relationship ($p < 0.001$) and a goodness of fit ($r^2 \geq 0.10$ along Axis 1 and/or Axis 2. Species are represented by the following letter codes: Aa *Ammophila arenaria,* Am *Achillea millefolium*, As *Agrostis stolonifera*, Bp *Bellis perenis*, Bry Bryophytes, Cn *Carex nigra*, Cf *Cerastium fontanum,* Eo *Euphrasia officinalis,* Gv *Galium verum*, Hs *Heracleum sphondylium*, Hc *Holcus lanatus*, Km *Koeleria macrantha*, Lic *Lichens*, Lc *Lotus corniculatus*, Luc *Luzula campestris*, Po *Pilosella officinale*, Pl *Plantago lanceolata*, Pp *Poa pratensis*, Pa *Potentilla anserina*, Pv *Pruna vulgaris,* Ra *Ranuculus acris*, Rr *Ranunculus repens*, Sj *Sencio jacobea*, Thp *Thymus polytrichus,* Tp *Trifolium pratense*, Tr *Trifolium repens*. b) Management determinants. c) Climatic and local environmental determinants. d) Broad-scale spatial determinants. e) Meso-scale spatial determinants. f) Small+Fine-scale spatial determinants.

2.3.4 Spatial scale of significant environmental correlates

Biplots of the RDA analysis used in the variation partitioning of response matrix (Y^f) revealed environmental determinants, in particular climatic predictors to be strongly correlated along Axis 1 (Figures 2.4c). Moreover, PET (a significant climatic predictor identified by stepwise selection; Table 2.4) and spatial variable 'pcnm1' (SAC = 153.5 km; Table 2.3), revealed a strong positive correlation with Axis 1 (Fig. 2.4d), suggesting Axis 1 to be representative of a longitudinal ecological gradient. Vegetation structure (<20cm) revealed a negative correlation with Axis 1. Other vegetation structure measures were partially correlated positively with Axis 1 and Axis 2, and revealed more similarity with fine-scaled spatial variable 'pcnm53' (SAC 1.5km). Measures of shrubs (Shr50.2m) correlated with presence of *Calluna vulgaris* (Figures 2.4 a-b) and revealed a positive correlation with Axis 1 and a negative correlation with Axis 2. The latter was well represented by broad-scale spatial variable 'pcnm6' (SAC = 70.5km) and meso-scale spatial variables 'pcnm14' and 'pcnm16' (SAC = 22.5km and 12.5km respectively).

Broad-scale spatial structuring of climatic variables among the Machair subset data (Y^S) showed identical patterns to that found for the full dataset. PET and 'pcnm1' (SAC = 94.5km) were both strongly and negatively correlated with Axis 2 (Figures 2.5c-d). Measures of precipitation (TP; Dsp1), along with GDU and sun duration were correlated with spatial variable 'pcnm2' (SAC = 140.5km), revealing a negative correlation with Axis 2. Significant management determinants such as vegetation structure greater than 20cm revealed a negative correlation with Axis 1 and displayed no association with any of the spatial variables.

2.4 Discussion

This Chapter presents how spatial eigenvectors derived through the PCNM approach, as proposed by Borcard and Legendre (2002), can be used within a variation-partitioning framework to identify scale-specific contributions of processes governing plant species composition of an important national resource. Three groups of environmental determinants and a fourth group of spatial determinants (PCNMs) were assessed in terms of their ability to explain variation in species composition on two species data matrices. First was a full-scale national dataset covering almost the entire resource of soft-coast sites across Scotland, and second, a subset, focusing specifically on the globally-rare biotype Machair grassland. For both datasets, the environmental and spatial determinants explained around 20% of the variation in species composition. Total variation explained (TVE) in this study is comparable with values reported for other, similar national-scale surveys of different vegetation classifications. For example, Corney et al. (2006) revealed TVE for national scale variation in field layer vegetation of different forest types ranged from 2.0-19.7%. Indeed, Økland (1999) suggests values between 20-50% are to be expected for TVE in constrained ordinations.

2.4.1 Environmental predictors

Management variables were found to capture more of the variation in plant species composition than other environmental predictors for both response matrices. Selection of model variables identified descriptors of vegetation structure, i.e. proxies for several determinants of vegetation composition such as grazing intensity and disturbance, to perform best in explaining this variation, reaffirming the relative importance of disturbance, typically through livestock grazing for the conservation management of dune grasslands (Oosterveld 1985; Aptroot et al. 2007; Plassmann et al. 2010). However, among both response matrices, variation partitioning identified management as also having the largest independent fraction of variation in species composition, suggesting that selected spatial PCNM variables failed to capture the spatial structure of these important management determinants.

For both response matrices, partial regression identified some degree of spatial structuring at the broadest scale, much of which was attributable to climate, while at the respective small and finer scales management was poorly represented by the spatial component. It is very probable, that scale-dependent management-induced patterns of coastal dune vegetation operate at a spatial grain much finer than this study could identify. Particularly in the Machair, the grasslands that lie behind the dune ridge were traditionally managed as small-scale rotational arable agriculture, involving small strips of land, cropped and then fallowed for a minimum of 2 years. Furthermore, the land was apportioned and managed by multiple tenants. The result was an extremely heterogeneous landscape of a mosaic of crops and fallows of different ages over relatively short distances. Niche processes as a result of land use constraints are therefore likely to operate at a much finer-scale relative to this constrained study design, and thus the results are likely to underestimate the influence of environmental heterogeneity on the vegetation composition of Scottish coastal grasslands.

Niche processes were however, also evident at the broadest scale, where climatic determinants were entirely spatially structured, capturing a significant proportion of the variation among both response matrices. Potential evapo-transpiration and humidity were selected as the best climatic descriptors of species composition for both response matrices and were found to correlate with broad-scale spatial variable pcnm1. Broad-scale PCNM variables likely represent large-scale geographical differences in vegetation composition, as might be expected for a national-scale vegetation survey of an extensive resource. Within Scotland, the climate becomes increasingly oceanic with increasing westerly longitude, with high humidity and precipitation. Therefore compared to the east coast, the western seaboard of Scotland is subject to very different climatic regimes, particularly true for areas of the Outer Hebrides where a hyper-oceanic climate exists. Large-scale latitudinal gradients may also be represented by the broad-scale PCNMs. Growing season is greater for southerly sites such as those of the Inner Hebrides (e.g. Islay) compared to those of Shetland and Orkney. Represented by Growing Degree Units (GDU), growing season length was identified as a significant climatic determinate, more so for the Machair dataset, where the longitudinal gradient is less severe. Such climatic gradients are likely to explain the shared fraction of variance between climate, management and broad-scale PCNM variables among both response matrices, as growing season length will influence vegetation structure. Among the full dataset, this 3-way shared fraction is likely to represent the difference in management between the Machair and non-Machair regions. However, it may also reflect the significant different in vegetative states between the east and west, as overall mean percentage cover of shrubs and tree species was far greater along the east coast sites compared to those on the west (Appendix 2.1). This results from deliberate attempts to stabilise many dune systems on the east through afforestation during the 20th century, e.g. Culbin Sands, northeast Scotland (Ovington 1950), an option not feasible on the west coast.

2.4.2 Spatial predictors

The spatial component for both response matrices explained circa 11% and 9% of the variation in species composition, where approximately two-thirds was shared with the environmental determinants, predominantly climate, while the remaining one-third was independent of all measured environmental predictors and theoretically represents pure spatial auto-correlation. However, the methodology used in this study relies heavily on the strength of the environmental variables selected for analyses (Laliberté et al. 2009). If the environmental component is inadequately described, the pure spatial fraction may represent unmeasured, spatially-structured environmental determinants (Borcard and Legendre 1994; Laliberté et al. 2009). It is probable then, for the broad-scale fraction, independent of measured environmental determinants, to reflect unmeasured variables such as soil chemical properties and or exposure, and as a result these analyses may have underestimated the importance of environmental heterogeneity in explaining spatial structures.

Fractioning the independent spatial contribution identified portions of true space in terms of their relative scale. Although the largest fractions of the 'true' spatial component were shown to be broadly-scaled for both response matrices, smaller fractions attributable to meso- and finer-scales suggest environmental heterogeneity may not be the sole processes governing vegetation composition across Scotland's soft coasts or Machair communities. The true spatial fractions across these scales revealed a small yet significant fraction within the context of the TVE. It is possible, particularly at very fine scales, for variation to be attributable to biotic/stochastic processes. The plausibility of which biotic processes is, however, governed by the spatial grain (resolution) of the dataset. In this study, the nearest neighboring sample location was circa 30 m, and in many cases often larger. Spatially-scaled biotic processes such as dispersal, facilitation or competition can exhibit much finer spatial scales than sampled in this study, and would require a study design with a fine spatial grain and spatial lag to detect. Therefore, at this resolution it is unlikely for many biotic processes to have been detected. Nevertheless, it is feasible at this relative fine scale for neutral processes such as long distance seed dispersal to be in operation, and thus the only plausible biotic processes to be captured by fine-scale PCNM variables. However, it is also very possible for environmental heterogeneity to govern vegetation patterns at this scale, particularly among the Machair habitats whereby land use results in an extremely heterogeneous landscape across relatively short distances.

2.4.3 Unexplained variation

The majority of the unexplained variance is likely to be due simply to lack-of-fit of data to the response model (Økland 1999). Measured descriptors of management do not include information on important descriptors of livestock density, fertilization or dates of cutting. Similarly the climatic parameters used in this survey are ones that are easily measurable by humans, and not necessarily ones that best describe plant distributions. Furthermore, the management predictors are simply a snapshot and do not cover historical practices that would have contributed to the vegetation patterns. For example: a recent study by Gustavsson et al. (2007) revealed that information on historic land use was necessary to understand present day diversity patterns of agricultural grassland biodiversity. Indeed, they showed, that historic land use information was a better determinant of current biodiversity patterns than more recent or current information of land use management. Finally, there is no information on soil chemistry included in this study (as the data did not survive the intervening years) and therefore nothing telling the model about the distribution of species according to pH, water, and soil nutrients, all-important drivers of species distributions. Large gradients in soil chemistry are known to be present in this dataset (Lennon et al. 2011). East coast sites typically include lime-poor, acidic substrates, whereas the western ones are renowned for their highly calcareous dune systems. Such broad gradients are likely to have been detected, captured by the independent broad-scale spatial fraction. However, soil chemistry can also be highly heterogeneous at much finer scales (Lennon et al. 2011). Given the heterogeneous nature of coastal dune systems, particularly Machair over relatively short distances, it is therefore likely that the majority of unexplained variation to result from biotic and abiotic processes operating upon the vegetation composition at scales much finer than the spatial resolution of this study.

2.5 Conclusions

The inclusion of a spatial component in the analysis of spatial patterns of plant species composition helped identify environmental and potential biotic processes and their relative importance in determining plant species variability across different spatial scales. Multi-scale analysis suggests species community composition of Scotland's soft coasts and Machair grasslands is maintained primarily through niche partitioning at the broadest scale. However management was poorly represented, suggesting niche processes as a result of land use constraints are likely to also operate at much finer scales, second to climatic filtering and at a scale outside the spatial resolution of this study. Similarly, the spatial resolution constrained the analyses from revealing whether biotic process played an equally predominate role in shaping the vegetation at truly fine-scales. However it is possible that independent spatial fractions identified at the finest scale represent seed dispersal mechanisms, while they may equally represent unmeasured spatially-scaled determinants such a soil chemistry. The results illustrate the potential of the methods described in dissecting the scale-specific importance of environmental and spatial variables on β-diversity for the conservation management of a national resource.

REFERENCES

Angus, S. 2006. De the Machair? Towards a Machair definition. Sand dune machair 4, 7-22. Aberdeen Institute for Coastal Science and Management, Aberdeen.

Anon. 2008. UK biodiversity action plan priority habitat descriptions: Machair. JNCC. Peterborough.

Aptroot, A., van Dobben, H.F., Slim, P.A., Olff, H. 2007. The role of cattle in maintaining plant species diversity in wet dune valleys. Biodiversity Conservation 16, 1541-1550.

Barot S and Gignoux J. 2004. Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? Oikos 106, 185-192.

Blanchet, F.G., Legendre, P., Borcard, D. 2008. Forward selection of explanatory variables. Ecology 89, 2623-2632.

Borcard, D. and Legendre, P. 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). Environmntal and Ecological. Statistics 1, 37-61.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045-1055.

Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153, 51-68.

Borcard, D. and Legendre, P. 2004. SpacemakeR 2. Department de Sciences Biologiques, Universite de Montreal.

Borcard, D., Legendre, P., Avois-Jacquet, C. and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85, 1826-1832.

Bunce, R.G.H. and Shaw, M.W. 1973. A standardized procedure for ecological survey. Journal of Environmental Management 1, 239-258.

Carvalho, J.C., Cardoso, P., Crespo, L.C., Henriques, S., Carvalho, R. and Gomes, P. 2011. Determinants of beta diversity of spiders in coastal dunes along a gradient of mediterraneity. Diversity and Distributions 17, 225-234.

Corney, P.M., Le Duc, M.G., Smart, S.M., Kirby, K.J., Bunce, R.G.H. and Marrs, R.H. 2006. Relationship between the species composition of the forest field layer vegetation and environmental drivers, assessed using a national scale survey. Journal of Ecology 94, 383-401.

Dargie, T.C.D. 2000. Sand dune vegetation survey of Scotland: National Report. Scottish National Heritage, Perth.

Dray, S., Legendre, P. and Peres-Neto, R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196, 483-493.

Gazol, A. and Ibañez, R. 2010a. Plant species composition in a temperate forest: Multi-scale patterns and determinants. Oecologica 36, 634-644.

Gazol, A. and Ibañez, R. 2010b. Variation of plant diversity in a temperate unmanaged forest in northern Spain: behind the environmental and spatial explanation. Plant Ecology 207, 1-11.

Gustavsson, E., Lennartsson, T. and Emanuelsson, M. 2007. Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biological Conservation 138, 47-59.

Hagreaves, G.H. and Samani, Z.A. 1985. Reference crop evapotranspiration from temperature. Applied Engineering in Agriculture 2, 96-99.

Hernandez-Stefanoni, J.L., Dupuy, J.M., Tun-Dzul, F. and May-Pat, F. 2011. Influence of landscape structure and stand age on species density and biomass of a tropical dry forest across spatial scales. Landscape Ecology 26, 355-370.

Hill, M.O. 1993. TABLEFIT, Version 1.0 for Identification of vegetation types. Institute of Terrestrial Ecology, Huntingdon.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hutchinson G. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantative Biology 22,415-427.

Kent, D.H. 1992. List of vascular plants of the British Isles. Botanical Society of the British Isles, London.

Laliberté, E., Paquette, A., Legendre, P. and Bouchard, A. 2009. Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. Oecologia 159, 377-388.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659-1673.

Legendre, P. and Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

Legendre, P., Borcard, D. and Peres-Neto, P.R. 2005. Analyzing beta diversity: Partitioning the spatial variation of community composition data. Ecological monographs 75, 435-450.

Lennon, J.J., Beale, C.M., Reid, C.L., Kent M. and Pakeman, R.J. 2011. Are richness patterns of common and rare species equally well explained by environmental variables? Ecography 34, 529-539.

Levin, S.A. 1992. The problem with pattern and scale in ecology. Ecology 73, 1943-1967.

Økland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. Journal of Vegetation Science 10, 131–136.

O'Briain, M. 2005. EU biodiversity policy context for the conservation of estuaries and dunes. In: Herrier, J.L., Mees, J., Salman, A., Seys, J., van Nieuwenhuyse, H., Dobbelaere, I. (eds) Dunes and Estuaries 2005 proceedings. pp. 7-12. International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium, 2005. VLIZ Special Publication 19. Flanders Marine Institute (VLIZ), Oostende, BE.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, R.B. 2007. vegan: community ecology package. R package version 1.9-25. http://cran.r-project.org/.

Oosterveld, P. 1985. Grazing in dune areas: the objectives of nature conservation and the aims of research for nature conservation management. In: Doody, J.P. Sand dunes and their management. pp. 187-203. Nature Conservancy Council, Peterborough, UK.

Ovington, J. 1950. The afforestation of the Culbin Sands. Journal of Ecology 38, 303–319.

Pakeman, R.J., Huband. S., Kriel. A. and Lewis. R.J. 2011. Changes in the management of Scottish Machair Communities and Associated Habitats from the 1970s to the Present. Scottish Geographical Journal. 127, 67-287.

Perry, M. and Hollis, D. 2005. The development of a new set of long-term climate averages for the United Kingdom. International Journal of Climatology. 25, 1023-1039.

Plassmann, K., Laurence, M., Jones, M. and Jones, G.E. 2010. Effects of long-term grazing management on sand dune vegetation of high conservation interest. Applied Vegetation Science 13, 100-112.

Pottier, J., Bedecarrats, A. and Marrs, R.H. 2009. Analysing the spatial heterogeneity of emergent groups to assess ecological restoration. Journal of Applied Ecology 46, 1248-1257.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (http://www.R-project.org).

Ribeiro JR. and Diggle, P.J. 2001. geoR: A package for geostatistical analysis. R-NEWS Vol 1, No 2. ISSN 1609-3631

Rodwell, J.S. 1991a. British plant communities. Volume 1: Woodlands and scrub. University Press Cambridge.

Rodwell, J.S. 1991b. British plant communities. Volume 2: Mires and heaths. University Press Cambridge.

Rodwell, J.S. 1992. British plant communities. Volume 3: Grasslands and montane communities. University Press Cambridge.

Rodwell, J.S. 2000. British plant communities. Volume 5: Maritime communities and vegetation of open habitats. University Press Cambridge.

Shaw, M.W., Hewett, D.G. and Pizzey, J.M. 1983. Scottish coastal survey. Institute of Terrestrial Ecology. Bangor Research Station, Bangor, Gwynedd.

Soinenen, J., Lennon, J.J. and Hillebrand, H. 2007. A multivariate analysis of beta diversity across organisms and environments. Ecology 88: 2830-2838

Ter Braak, C.J.F. and Šmilauer, P. 2002. CANOCO reference manual and Canodraw for Windows user's guide: software for canonical community ordination version 4.5. Microcomputer Power, Ithaca, NY.

Thornthwaite, C.W. 1948. An approach towards a rational classification of climate. Geographical Review 38, 55-94.

Wagner, H.H. 2003. Spatial covariance in plant communities: integrating ordination, geostatistics, and variance testing. Ecological Society of America 84, 1045-1057.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30, 279–338.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21, 213-251.

Wiens, J.A., Addicott, J.F., Case, T.J. and Diamond, J. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. In: Diamond, J. and Case, T.J. (eds) Community ecology, pp .145-153. Harper and Row, New York.

Appendix 2.0

Appendix 2.1 Site Information.

Site	Site Name	Easting	Northing	Region	Island	No.Plots	Avg Shrub Cover (%)	Avg Tree Cover (%)
1	Torrs Warren	210888	552381	SOUTH WEST	SOLWAY	110	24	12
2	Macrihanish	165503	625850	SOUTH WEST	ARGYLL	42	0	0
3	Laggan	132491	652964	INNER HEBRIDES	ISLAY	44	18	4
4	Machir Bay	120645	662361	INNER HEBRIDES	ISLAY	30	0	0
5	Saligo bay	121998	667165	INNER HEBRIDES	ISLAY	30	3	0
6	Gruinart	129235	674787	INNER HEBRIDES	ISLAY	70	12	3
7	Oronsay	134768	686835	INNER HEBRIDES	COLONSAY	44	11	1
8	Garvard	136412	690561	INNER HEBRIDES	COLONSAY	32	15	6
9	Kiloran	141176	697812	INNER HEBRIDES	COLONSAY	35	9	3
10	Calgary	137237	751370	INNER HEBRIDES	MULL	30	1	0
11	Sanna	144077	769358	MAINLAND	WEST	30	0	15
12	West Tiree	95444	740782	INNER HEBRIDES	TIREE	102	3	4
13	North Tiree	97910	748275	INNER HEBRIDES	TIREE	40	0	0
14	Crossapoll	98414	741887	INNER HEBRIDES	TIREE	36	0	0
15	West Coll	115040	753333	INNER HEBRIDES	COLL	100	8	6
16	Clabhach	117087	757524	INNER HEBRIDES	COLL	36	0	5
17	Gallawach	124540	763533	INNER HEBRIDES	COLL	46	4	3
18	Vatersay	61784	797046	WESTERN ISLES	BARRA	26	0	0
19	West Barra	65742	804285	WESTERN ISLES	BARRA	39	0	0
20	N Barra	69134	805513	WESTERN ISLES	BARRA	45	1	0
21	Daliburgh	72636	827485	WESTERN ISLES	S.UIST	64	0	1
22	Ormiclate	73664	833219	WESTERN ISLES	S.UIST	56	0	0
23	Howbeg	74315	835315	WESTERN ISLES	S.UIST	32	0	0
24	Stiligarry North	75557	839844	WESTERN ISLES	S.UIST	36	1	0
25	Loch Bee	76594	842248	WESTERN ISLES	S.UIST	94	6	0
26	Borve	78345	849205	WESTERN ISLES	BENBECULA	30	0	0
27	Stilligarry	75595	839748	WESTERN ISLES	S.UIST	42	7	0
28	Baleshare	79356	858112	WESTERN ISLES	BALESHARE	64	0	0
29	Kirkibost	76841	865167	WESTERN ISLES	KIRKIBOST	28	0	0
30	Monach Isles	60316	862217	WESTERN ISLES	MONACH ISLES	40	0	0
31	Paible	72230	869002	WESTERN ISLES	N.UIST	32	0	0
32	Hosta	71021	872728	WESTERN ISLES	N.UIST	36	10	0

Appendix 2.1 Continued..

Site	Site Name	Easting	Northing	Region	Island	No.Plots	Avg Shrub Cover (%)	Avg Tree Cover (%)
33	Vallay	79478	876973	WESTERN ISLES	N.UIST	32	20	0
34	Leathann	79887	875464	WESTERN ISLES	N.UIST	54	0	0
35	Balranald	69137	871005	WESTERN ISLES	N.UIST	41	0	1
36	Robach	85529	875935	WESTERN ISLES	N.UIST	46	0	5
37	Berneray	88738	880511	WESTERN ISLES	BERNERAY	68	0	27
38	Pabbay	87178	887961	WESTERN ISLES	PABBAY	62	6	4
39	Northton	101039	893834	WESTERN ISLES	HARRIS	32	3	1
40	Luskintyre	106738	900090	WESTERN ISLES	HARRIS	30	0	0
41	Uig	100907	930827	WESTERN ISLES	LEWIS	28	26	1
42	Valtos	108060	936185	WESTERN ISLES	LEWIS	27	0	0
43	Barvas	134009	950574	WESTERN ISLES	LEWIS	30	21	0
44	Europie	153232	963876	WESTERN ISLES	LEWIS	30	0	0
45	Tolsta	153290	948834	WESTERN ISLES	LEWIS	30	1	0
46	Tong	145698	934215	WESTERN ISLES	LEWIS	30	0	0
47	Quendale	438170	1113013	SHETLAND	SHETLAND	35	0	0
48	Scousburgh	437686	1117741	SHETLAND	SHETLAND	30	0	0
49	Breckon	453650	1204978	SHETLAND	SHETLAND	26	23	0
50	Red Point	172543	868630	MAINLAND	NORTH WEST	42	11	4
51	Holland	362594	1037280	ORKNEY	ORKNEY	31	0	0
52	Achnahaird	202183	912804	MAINLAND	NORTH WEST	27	10	2
53	Oldshore More	219883	959293	MAINLAND	NORTH WEST	42	9	3
54	Sheigra	218098	960034	MAINLAND	NORTH WEST	42	7	8
55	Durness	237646	966321	MAINLAND	NORTH WEST	28	4	2
56	Faraid Head	239092	971738	MAINLAND	NORTH WEST	35	0	1
57	Bettyhill	268452	961136	MAINLAND	NORTH WEST	33	7	2
58	Farr Bay	271561	962775	MAINLAND	NORTH	42	0	0
59	Strathy	283690	965171	MAINLAND	NORTH	28	6	29
60	Melvich	288152	965310	MAINLAND	NORTH	36	24	3
61	Reay	295935	965348	MAINLAND	NORTH	42	0	0
62	Dunnet	323926	971940	MAINLAND	NORTH EAST	42	3	23
63	Freswick	337193	967790	MORAY FIRTH	NORTH EAST	42	0	0
64	Sandwood	221246	964785	MAINLAND	NORTH WEST	42	7	10
65	Sinclair's bay	334154	960097	MORAY FIRTH	NORTH EAST	36	0	0
66	Ferry links	280667	895963	MORAY FIRTH	MORAY FIRTH	46	18	43
67	Coull Links	280823	895332	MORAY FIRTH	MORAY FIRTH	42	9	9

Appendix 2.1 Continued..

Site	Site Name	Easting	Northing	Region	Island	No.Plots	Avg Shrub Cover (%)	Avg Tree Cover (%)
68	Dornoch	280554	888898	MORAY FIRTH	MORAY FIRTH	36	0	0
69	Clashmore	275770	887732	MORAY FIRTH	MORAY FIRTH	36	23	0
70	Morrich More	280766	883852	MORAY FIRTH	MORAY FIRTH	45	20	5
71	Whiteness	280235	858772	MORAY FIRTH	MORAY FIRTH	42	16	2
72	Culbin bar	299182	864470	MORAY FIRTH	MORAY FIRTH	44	22	6
73	Overbister	371626	1041924	ORKNEY	ORKNEY	32	0	0
74	Findhorn	303688	864940	MORAY FIRTH	MORAY FIRTH	35	16	21
75	Lossiemouth	324364	869914	MORAY FIRTH	MORAY FIRTH	39	10	62
76	Spey Bay West	332147	866235	MORAY FIRTH	MORAY FIRTH	38	17	14
77	Spey bay central	334185	865722	MORAY FIRTH	MORAY FIRTH	44	16	19
78	Spey Bay East	335674	864794	MORAY FIRTH	MORAY FIRTH	24	20	36
79	Fraserburgh	400235	865760	EAST COAST	NORTH EAST	35	0	0
80	Strathbeg	410335	858198	EAST COAST	NORTH EAST	64	3	10
81	St Fergus	411497	849163	EAST COAST	NORTH EAST	46	0	0
82	Cruden Bay	409215	836041	EAST COAST	NORTH EAST	30	0	0
83	Forvie	400662	824569	EAST COAST	NORTH EAST	89	25	12
84	Balmedie bay	400257	824452	EAST COAST	NORTH EAST	58	17	7
86	St. Cyrus	372599	757735	EAST COAST	EASTERN LOWLNADS	53	14	24
87	Lunan Bay	369354	752163	EAST COAST	EASTERN LOWLNADS	32	37	1
88	Arbroath	360237	737002	EAST COAST	EASTERN LOWLNADS	30	15	0
89	Barry Links	350335	732343	EAST COAST	EASTERN LOWLNADS	120	9	23
90	Tentsmuir	347515	723469	EAST COAST	EASTERN LOWLNADS	87	6	13
91	Dumbarnie	344390	702100	EAST COAST	EASTERN LOWLNADS	30	0	0
92	Aberlady	366593	677121	EAST COAST	EASTERN LOWLNADS	31	0	4
93	Gullane	346960	683069	EAST COAST	EASTERN LOWLNADS	46	1	7
94	Yellowcraig	352863	685393	EAST COAST	EASTERN LOWLNADS	30	0	1
95	Tyninghame	362057	682118	EAST COAST	EASTERN LOWLNADS	35	0	6

Supplementary Material (S2)

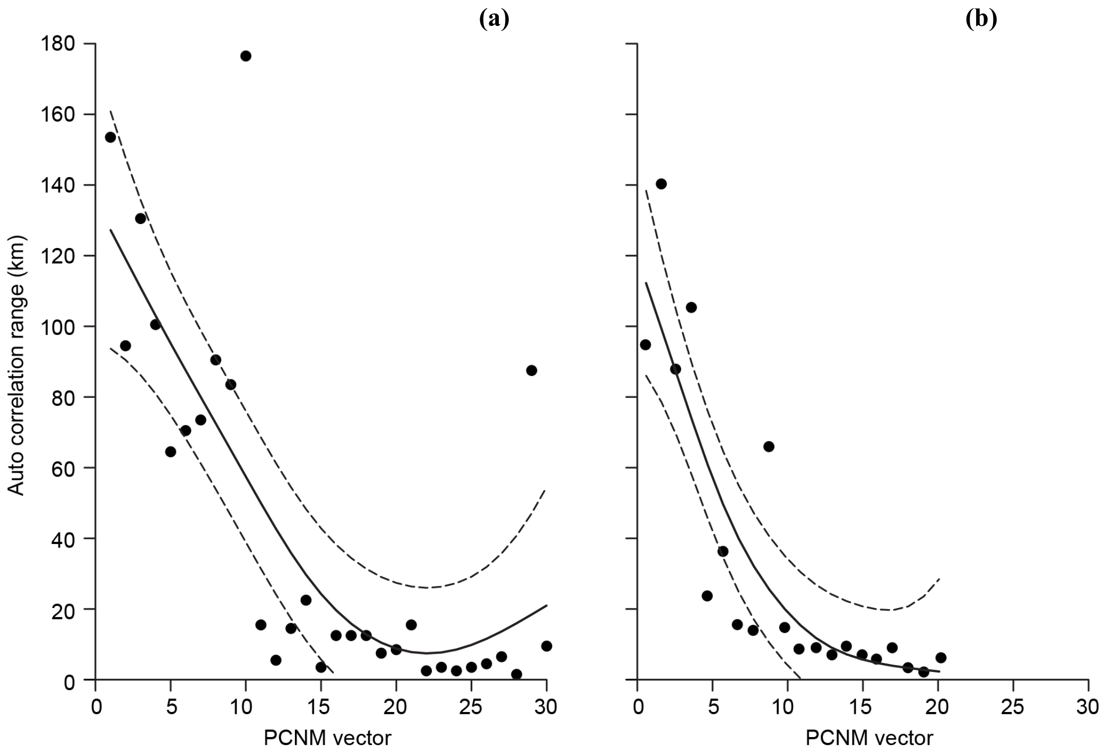


Fig. S2.1 Plot of selected PCNM variables against spatial autocorrelation range values for the (a) full ($\mathbf{Y}^f$) and (b) the Machair ($\mathbf{Y}^s$) sub-set data of quadrats sampled in Scottish soft coasts. These were obtained by fitting experimental variograms to each derived PCNM variable. Solid and dashed lines denote best fit and upper and lower confidence limits.

Chapter Three

Identifying national-scale drivers of species compositional change in Scottish Machair over a 30-year period: A revisitation study

ABSTRACT

Certain habitats, such as semi-natural grasslands, have shown substantial resistance to climate change, but are known to be sensitive to changes in land use and management. A re-survey of the entire national resource of Scottish Machair habitat including its associated grasslands (i.e. globally-rare habitats of high conservation and national heritage importance) was used to assess changes in vegetation driven by land use management and climate. The aim of the study was to identify national- and regional-scale temporal vegetation patterns, and relate them to drivers of change in order to highlight specific regions of potential conservation concern. Vegetation change was quantified using indirect ordination, as well as by comparison of Ellenberg Indicator Values (IVs) and plant functional signatures (CSR). Results suggest a considerable national-scale change in vegetation composition of the Machair system and Machair grassland habitats, with an overall national gain in species richness per quadrat. Regional-scale analyses identified several islands (Barra, Coll, Colonsay, Islay, South Uist and Tiree) that displayed significant gains in biodiversity, including gains in species indicative of good quality Machair grassland (largely islands that were designated as Environmentally Sensitive Areas). Regional gains and falls were recorded for species indicator and functional signature scores attributable to varying degrees of internal (competition) and external (land use and climatic) factors. Highlighted are several regions where biodiversity decline can be linked to either reduced disturbance, particularly grazing intensity (Benbecula, Harris, Monachs and North Uist), or more intensive disturbance (Shetland). Results also indicate (1) an increase in nitrophilous species supporting claims of an overall shift towards use of inorganic fertilisers, and (2) an overall decline in wetland specialists suggestive of substantial drying out of the Machair habitats.

The conservation value of the Machairs are clearly sensitive to land use change. Here, regions are identified as showing either improvement in Machair quality or declines. The conservation importance of financial incentives to maintain ecologically beneficial land use practices that are otherwise socially and economically unviable is evident. This study highlights the usefulness of revisitation studies for informing national-scale conservation policies and determining priorities for action. Furthermore it demonstrates the utility of species indicator and functional values for attributing drivers of observed vegetation change.

3.1 Introduction

Investigating the effects of changing biodiversity within the realm of human-induced climate change is often at the forefront of ecological investigations and has become a major contemporary issue in ecology (Parmesan and Yohe 2003; Thomas et al. 2004a). Evidence of changing climatic conditions is well documented both globally and within a UK context (IPCC 2007; Jenkins et al. 2007), leading to concerns that long-term changes will drive changes in plant community composition and structure, altering ecosystem function and altering the ability of ecosystems to adapt to future environmental change (Chapin et al. 2000).

However, for certain terrestrial habitats such as grassland ecosystems, land use may be a more important driver of such biodiversity change (Sala et al. 2000). For these ecosystems, land use interactions with climate and other anthropogenic factors may be more of a threat than climate change alone (Grime et al. 2008).

Understanding the nature of vegetation change over time is paramount to the appropriate design of nature conservation practices, policies and land management across local, regional and national scales. Revisitation studies, using archived biological records have the potential to quantify long-term vegetation change (McCollin et al. 2000; Bennie et al. 2006; McGovern et al. 2011). Providing the relocation of plots can be achieved with reasonable confidence (Ross et al. 2010), these snapshots of vegetation composition over time provide valuable data necessary for the detection of species composition and diversity change. Moreover, revisitation data, coupled with environmental indicator values such as Ellenberg values (Hill et al. 1999) and/or plant strategies (Grime 1974), can help to attribute drivers to observed patterns of change (Bennie et al. 2006; McGovern et al. 2011).

This Chapter investigates temporal data collected from a revisitation study of Scottish Machair; a distinctive and bio-diverse coastal biotype, confined solely to Scotland (30,000 ha) and Ireland (10,000 ha; Anon. 2008). It is globally unique to the north-western fringe of Europe, and is renowned for its ecological and national heritage importance (Angus 1994; Owen et al. 1996, 2000). Here, a distinction is made between the whole Machair system and Machair grassland (following Ritchie 1976 and Angus 2006). The Machair system includes all transient habitats from seaward embryo dunes to inland sand-affected peatlands termed ‘blacklands’, while ‘Machair grassland’ refers only to the relatively flat, low-lying, short turf grasslands, which in recognition of their floristic diversity and conservation value are listed on Annex I of the EC Habitats and Species Directive (Council Directive 92/43/EEC).

The conservation value of the Machair system is dependent on active management through traditional crofting and farming practices (Angus and Dargie 2002; Angus 2009). Agriculture on the Machair traditionally involved a form of small-scale rotational arable agriculture alongside livestock production. Crops (typically grain) were low yielding, small-scale and remained unfenced, often adjacent to fallows of (usually) 2 years duration. These crops were often fertilized with storm-cast seaweed (Angus and Dargie 2002; Angus and Hansom 2004); while use of herbicides was uncommon. Traditionally, cattle and sheep graze the hills and moorlands in the summer, and the lowland Machair grasslands in the winter (Caird 1979; Angus 2001). The result is a small-scale patchwork of habitats with high botanical and invertebrate biodiversity (Owen et al. 1996; Goulson et al. 2005; Redpath et al. 2010).

Machair communities are however, under threat. Socio-economic changes, including a declining and ageing population (Mackenzie 2007) and changes in agricultural subsidies, have resulted in some shifts away from traditional land management towards more modern and/or less time consuming agricultural practices. Machair vegetation has formed in close association with human activity and this is recognised through its natural heritage designations. However, changes in the management of the Machair system provide major concerns for the conservation value of this habitat. It is feared that a disruption to this fine balance between land use and the conservation and heritage value may be exacerbated by the interaction of other environmental drivers of change, and in particular, the pressures of future climate change scenarios (Angus and Hansom 2004).

This Chapter presents the results of a revisitation survey of Scottish Machair systems, including the Machair grasslands, from baseline data first collated in 1976. This study aims to (i) assess and summarise any change in the community composition within the Machair system and associated grasslands throughout the entire survey area (effectively a national scale survey); (ii) at the finer scale, to quantify and compare any changes within and between different geographic localities; and (iii) to relate any observed change in vegetation composition to changes in the external environment, using environmental indicator values to further support conclusions made linking vegetation shifts to land use and climatic change.

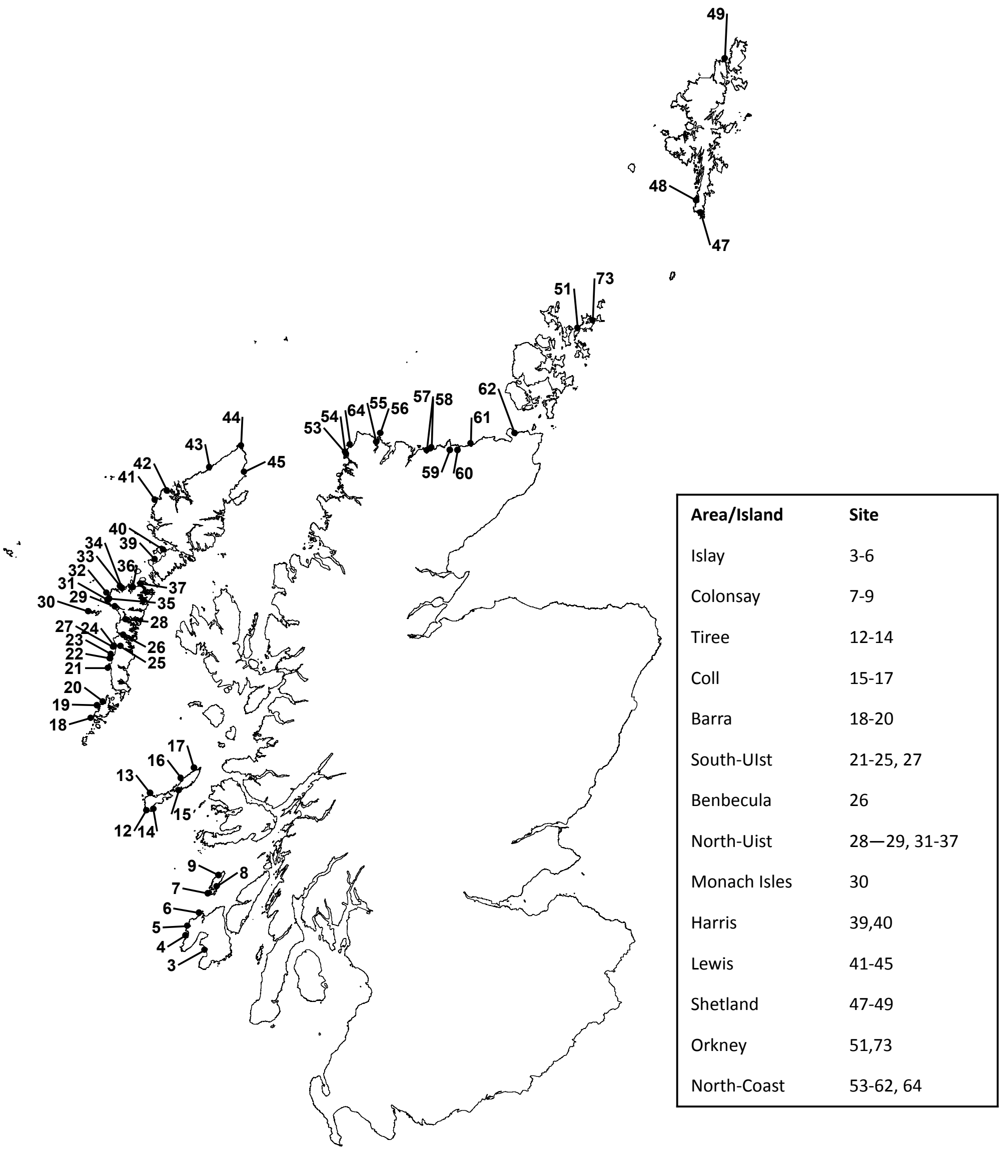
3.2 Materials and Methods

3.2.1 Study Area

The Scottish Coastal Survey of 1975 to 1977 (Shaw et al. 1983) formed the baseline data for this study. Of the 94 coastal sites originally surveyed, a sub-sample of 56 sites within regions known to include Machair and its associated landforms were selected for re-survey (Fig. 3.1).

3.2.2 Vegetation Survey

A vegetation re-survey of 1548 plots was undertaken between June and September 2009 (5 sites) and 2010 (51 sites). Number of plots per site ranged from 9 to 61 (Appendix 3.1). To minimise sources of error between surveys, sites were re-surveyed as close to the original survey date as possible. The position of the original plots were digitised from the original 1:10 000 maps, and relocated in the field using a hand-held global positioning system to within an estimated ± 10 m of the original position. The exact location of the plot was selected using information on the original vegetation composition. Where there was uncertainty over the original plot location, it was omitted from the survey. This method of revisitation surveying for non-permanent vegetation sampling has been shown to be effective in detecting temporal change with confidence (Ross et al. 2010).



Area/Island	Site
Islay	3-6
Colonsay	7-9
Tiree	12-14
Coll	15-17
Barra	18-20
South-UIst	21-25, 27
Benbecula	26
North-Uist	28—29, 31-37
Monach Isles	30
Harris	39,40
Lewis	41-45
Shetland	47-49
Orkney	51,73
North-Coast	53-62, 64

Fig 3.1 Distribution of study sites across Scotland. For site information see Appendix 3.1.

The survey methodology followed Shaw et al. (1983). Estimates of cover for all plant species and collective cover for bryophytes and lichens were recorded in every 5 m x 5 m quadrat by a team of trained surveyors. A number of local environmental variables were measured for each plot including past and present land use, current grazing intensity, presence/absence of grazing animals and categorical measures of sward height for grasses, herbs and shrubs (*see Supplementary material S3.3 for methods on how grazing pressure levels and past cultivation were determined*).

The UK Meteorological Office 5 km monthly gridded datasets, UKCP09 (Perry and Hollis 2005) were used for deriving long-term average (LTA) climatic variables. Baseline climate values for the original survey and the repeat survey were calculated for the years 1961 – 1977, and 1990 – 2006, respectively. Values for areas where climatic information was missing, were interpolated by taking a weighted average of its neighbours (i.e. neighbouring 5 km grid cells); temperature variables were adjusted by a lapse rate of 0.6°C/100 m, using altitudinal data derived from 1 km detailed digital terrain models. Four climate indices were calculated, describing the climate as a linear function of combined climatic parameters. These included relative measures of Oceanicity (Ellis and Coppins 2007), Potential Evapo-transpiration (PET, calculated after Hagreaves and Samani 1985), the Aridity index of Thornthwaite (1948) and Growing Degree Units encompassing a generic threshold temperature of 6°C (GDU; McMaster and Wilhelm 1997). The full suite of variables is given in Table S3.1.

To quantify the effects of environmental change on the vegetation composition of the Machair system and Machair grasslands, species data were summarised as indicator values and functional signatures for each plot (McGovern et al. 2011), acting as correlates for various climatic and land use changes. The CSR scheme of Grime (1974) and Grime et al. (1988) was used to calculate CSR functional signatures (Hunt et al. 2004); these scores provide an indication of external factors likely to alter plant growth, such as inter-specific competition for resources, stress through lack of plant available resources and disturbance. Cover-weighted Ellenberg indicator values (IVs) adjusted for British plants (Ellenberg 1988; Hill et al. 1999) were also calculated; here five IVs were used reflecting species preference in terms of nutrient level (EbN), acidity (EbR), moisture (EbW), light (EbL) and salinity (EbS). Finally, as an indirect measure of change in the management and Machair condition, four species indicator groups (SIG) were devised, comprising species indicative of good and poor quality Machair grassland, fallow areas (suggestive of continuous rotational arable agriculture) and active cultivation (Joint Nature Conservation Committee 2004; Table S3.2).

3.2.3 Statistical Analysis

Nomenclature follows Kent (1992), and old nomenclature was updated to current taxonomy (Stace 2010). Closely-related species, which are difficult to separate consistently, were combined at the genus level, i.e. *Euphrasia, Hieracium* and *Taraxacum* species. Bryophytes and lichens were given a collective abundance value and were each analysed as a single unit of percentage cover.

Data for 1548 plots were used to construct two datasets. The first (hereafter referred to as the 'Machair system') included 1548 plots and all habitats types from the shore to peatlands (i.e. strandline, saltmarsh, foredunes, dune-grassland, dune slacks, lochs, fens and blacklands). The second, containg 853 plots (hereafter referred to as 'Machair grassland') was a sub-set including only those plots with a National Vegetation Classification (NVC) known to be representative of Machair grassland. The latter was achieved by allocating all samples from the original survey a NVC class (Rodwell 1991a, 1991b, 1992, 2000) using the software package 'TABLEFIT' (Hill 1993). NVC communities typical of Machair grassland followed those defined by Angus (2006):

(i) SD8a *Festuca rubra-Galium verum* fixed dune grassland, typical sub-community

(ii) SD8c *Festuca rubra - Galium verum* grassland, *Tortula ruralis* ssp. *ruraliformis* sub-community

(iii) SD8d *Festuca rubra - Galium verum* fixed dune grassland*, Ranunculus acris - Bellis perennis* sub-community

(iv) SD8e *Festuca rubra - Galium verum* grassland, *Prunella vulgaris* sub-community

(v) MG11 *Festuca rubra – Agrostis stolonifera – Potentilla anserina* grassland

(vi) SD17 *Potentilla anserina - Carex nigra* dune slack, *Agrostis stolonifera* sub-community.

All statistical analyses were carried out in R (Version 2.11.0, R Development Core Team 2011). Change in species mean cover was compared between only those species recorded in both the original and re-survey. Initially, paired t-tests were used to detect change in overall species diversity and vegetation condition measures between the two sampling dates. To investigate whether a shift in community composition had occurred between years, principal component analyses (PCA) were conducted, following Hellinger transformation (Legendre and Gallagher 2001), using the vegan software package (Oksanen et al. 2009). Shifts in community composition at the area/island scale were measured by calculating the distance between PCA site scores for each survey year. The significance of these shifts was tested using linear-mixed modelling with residual maximum likelihood. 'year' and 'region' were fixed factors, while land-owner and individual plots were included in the model as nested random factors. The same model structure was used to test for significant differences between survey years for species diversity (GLMM, with Poisson link function), IV scores, CSR functional signatures and the mean cover of species indicator groups (SIG; JNCC 2004). The SIG analysis was confined to the Machair grassland only, whereby analyses investigated change in species representative of: (i) poor quality Machair grassland, (ii) good quality Machair grassland, (ii) fallowed areas and (iv) cultivated areas (see Table S3.2 for species lists). These analyses compared mean frequency and mean species cover using generalised linear and linear mixed models respectively, using the 'nlme' software package (Pinheiro et al. 2011) within the R statistical language framework. When necessary, data were transformed to meet assumptions of normality and homogeneity of variance.

3.3 Results

3.3.1 Community composition analysis

In 1976, 408 vascular plant species (269 Machair grassland) were recorded, compared with 398 species (278 Machair grassland) in 2010. Eighty-six species recorded in 1976 were not recorded in 2010, while similarly 73 previously unrecorded species were found in the 2010 survey; of these 39 (1976) and 35 (2010) were recorded only once. Sixteen plant species within the Machair system and 9 plant species within the Machair grassland showed large proportionate changes in percentage cover in the plots that they occupied in the original survey. Within the Machair system, *Dryas octopetala* and *Petasites hybridus* showed the greatest proportionate change (±SE) in cover of +20.38 ± 1.37 % and -37.0 ± 2.03 % respectively. Analyses of the Machair grassland revealed *Juncus gerardii* and *Centaurea scabiosa* to show the greatest proportionate change in cover; *J.gerardii* increased by 9.8 ± 2.37 % and *C.scabiosa* decreased by 21.0 ± 1.41 %. Others to reveal a substantial decline (i.e. > 5%) were *Phragmites australis*, *Equisetum palustre*, *Iris pseudacoras* and *Eleocharis uniglumis* all exclusively wetland species. Marked proportionate changes in bryophyte cover (+8.06 ± 0.004 % and +8.36 ± 0.01 %) were also recorded for both the Machair system and Machair grassland respectively (Fig. 3.2).

A significant increase in species richness (SR) was found for both the Machair system and Machair grassland (Table 3.1). Mean SR per plot increased from 21.6 ± 0.23 to 23.9 ± 0.21, and 22.4 ± 0.27 to 24.49 ± 0.24 for the Machair system and Machair grassland respectively. This pattern was found to diverge at the finer area/island scale. Barra, Coll, Colonsay, Islay, S.Uist and Tiree showed a significant increase in SR within both the Machair system and Machair grassland. Conversely, Harris, Lewis, Monachs and Shetland showed a significant drop in SR. The N.Coast and N.Uist revealed a significant fall in SR only within the Machair system and not in the Machair grassland.

3.3.2 Environmental drivers of change and community analysis

The first two PCA Axes for the Machair system and Machair grassland datasets explained approximately 23% of the total variation in species composition, a respectable proportion for studies of a national resource (Corney et al. 2006; Marrs et al. 2011). It was, however, difficult to identify noteworthy shifts in species composition over the two survey years from these ordinations (Fig. 3.3). It is probable the broad trends at the national-scale obscure changes at the finer-scale i.e. those specific to different geographical regions. Differences between years at the finer area/island scale were thus disentangled through REML analysis of PCA sites scores; this analysis identified significant overall changes between survey years for several regions among both datasets (Table 3.2). Significant shifts along Axis 1 and/or 2 (shifts denoted $^{(\text{Axis 1/Axis 2})}$ where · = no significant shift) were noted within the Machair system for Colonsay$^{(\cdot/-)}$, Harris$^{(\cdot/+)}$, Lewis$^{(+/\cdot)}$, Monachs$^{(\cdot/+)}$, N.Coast$^{(-/+)}$, N.Uist$^{(\cdot/+)}$, Sanday$^{(\cdot/-)}$, Shetland$^{(\cdot/-)}$ and Tiree$^{(\cdot/-)}$; and for the Machair grassland; Barra$^{(+/-)}$, Harris$^{(+/\cdot)}$, Lewis$^{(\cdot/-)}$, Monachs$^{(+/\cdot)}$, N.Coast$^{(\cdot/-)}$, N.Uist$^{(+/-)}$, Sanday$^{(-/\cdot)}$, and Tiree$^{(-/\cdot)}$ (Table 3.2).

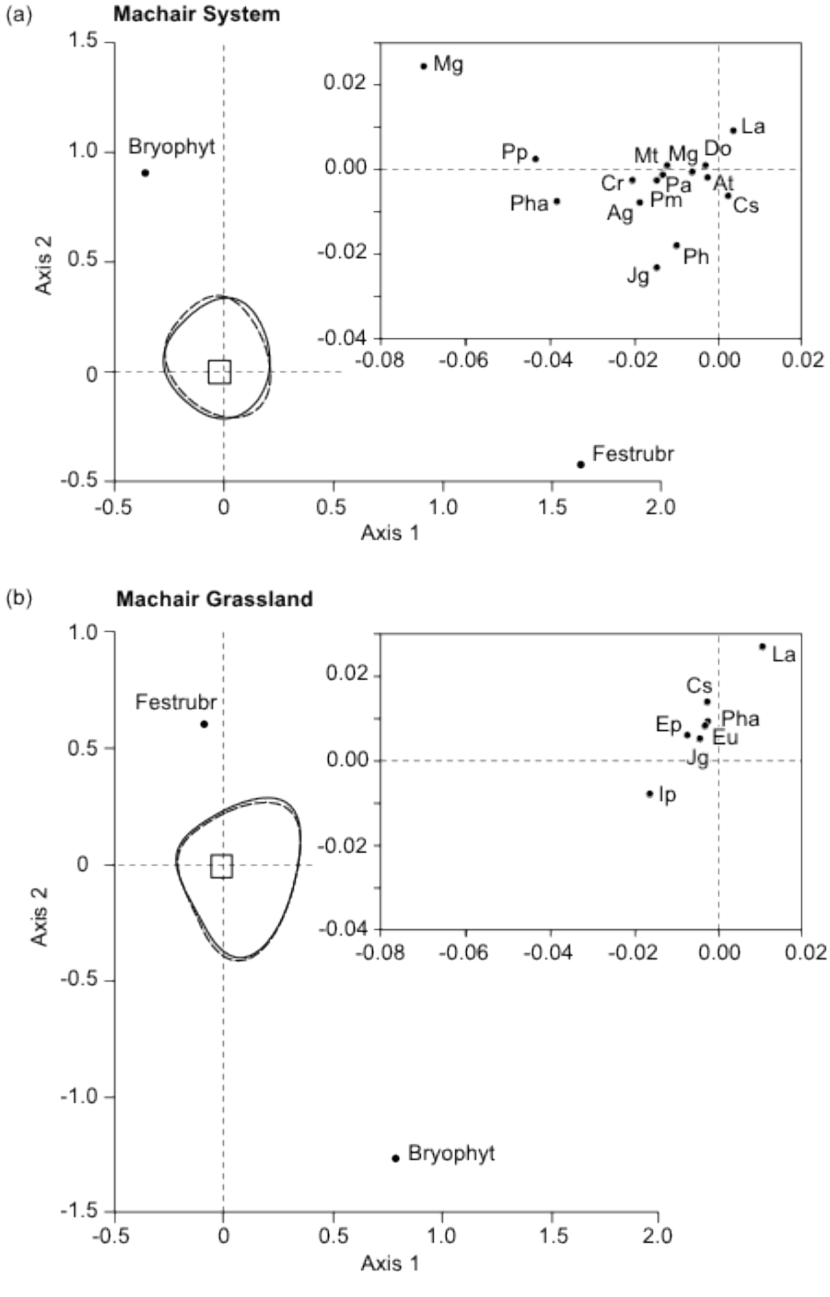


Fig. 3.2 PCA of vegetation composition: (a) Machair system and (b) Machair grassland. Displayed are the convex hulls for both survey years (dashed and solid lines refer to the survey years 1976 and 2010, respectively), enveloping all 1548 plots (Machair system) and 853 plots (Machair grassland). Species that have shown the greatest change in percentage cover (± 5%) are projected on top of the ordination. Abbreviations of species names and its compositional change (-ve or +ve) are as follows: Ag$^{(-)}$ *Alopecurus geniculatus,* At$^{(+)}$ *Aster tripolium,* Bryophyt$^{(+)}$ Bryophytes, Cr$^{(-)}$ *Carex rostrata,* Cs$^{(-)}$ *Centaurea scabiosa,* Do$^{(+)}$ *Dryas octopetala,* Eq$^{(-)}$ *Equisetum palustre,* Eu$^{(-)}$ *Eleocharis uniglumis,* Festrubr$^{(+)}$ *Festuca rubra,* Ip$^{(-)}$ *Iris pseudacorus,* Jg$^{(+)}$ *Juncus geradii*, La$^{(+)}$ *Leymus arenarius,* Mg$^{(-)}$ *Myrica gale,* Mt$^{(-)}$ *Menyanthes trifoliata,* Pa$^{(+)}$ *Phalaris arundinacea,* Pc$^{(+)}$ *Puccinellia maritima*, Pha$^{(-)}$ *Phragmites australis,* Ph$^{(-)}$ *Petasites hybridus,* Pp$^{(+)}$ *Potentilla palustre*, Tm$^{(+)}$ *Tripleurospermum maritimum*.

Table 3.1 Species diversity of Machair and Machair grassland vegetation in 1976 and 2010. Mean plot values (5 m x 5 m) with (+/-) SE in parentheses are displayed. (+/-) against area indicates overall increase or decrease in species richness, respectively. Asterisks indicate degree of significance of paired t-test (full datasets) and GLMM (Areas and Islands): <0.001 '***' 0.001 '**' 0.01 '*' 0.05 '.' >0.05 'n.s. '

	Machair System				Machair Grassland			
Areas	1976	2010	t	p	1970	2016	t	p
All (+)	21.63 (0.23)	23.92 (0.21)	9.45	***	22.39 (0.27)	24.49 (0.24)	6.84	***
			z				z	
Barra (+)	18.80 (1.00)	23.39 (1.08)	5.27	***	20.55 (0.81)	24.55 (1.09)	4.08	***
Benbecula (-)	20.65 (1.16)	19.10 (1.61)	-1.10	n.s.	21.57 (0.75)	18.36 (1.84)	-1.90	.n.s.
Coll (+)	17.98 (0.47)	27.80 (0.64)	15.7	***	16.78 (0.51)	26.78 (0.79)	12.4	***
Colonsay (+)	12.57 (0.65)	22.69 (1.05)	14.0	***	11.30 (1.13)	26.00 (1.20)	7.39	***
Harris (-)	21.90 (1.51)	19.59 (1.36)	-2.73	**	26.04 (1.59)	20.70 (1.57)	-3.74	***
Islay (+)	17.23 (0.57)	23.68 (0.75)	11.9	***	16.16 (0.66)	25.05 (0.82)	8.47	***
Lewis (-)	26.55 (0.88)	25.24 (0.62)	-2.00	*	28.76 (0.97)	26.54 (0.66)	-2.67	**
Monachs (-)	21.16 (0.83)	18.08 (0.83)	-2.99	**	21.34 (0.86)	18.26 (0.85)	-2.90	**
North Coast (-)	27.13 (0.65)	24.73 (0.54)	-5.29	***	28.01 (0.86)	26.51 (0.76)	-1.95	.n.s.
North Uist (-)	24.80 (0.55)	23.91 (0.52)	-2.06	*	25.55 (0.51)	24.94 (0.55)	-1.19	n.s.
Sanday (+)	21.02 (0.85)	21.42 (0.71)	0.46	n.s.	21.60 (0.81)	21.65 (0.72)	0.04	n.s.
Shetland (-)	20.68 (0.68)	19.06 (0.57)	-2.29	*	22.47 (0.90)	19.21 (0.64)	-2.94	**
South Uist (+)	19.65 (0.67)	24.62 (0.62)	10.4	***	18.59 (0.78)	22.94 (0.78)	6.66	***
Tiree (+)	17.34 (0.40)	26.76 (0.59)	14.3	***	17.18 (0.34)	27.24 (0.55)	13.7	***

Table 3.2 Results of REML analyses of PCA site scores for the Machair system and Machair grassland between survey years. Direction of shift between years along each axis can be inferred from the mean change values and t-values. A small negative value indicates a small negative shift along an axis, conversely a large positive value indicates a large positive shift. Values in bold indicate a significant difference between survey years $p < 0.05$

	PCA Axis 1 Scores			PCA Axis 2 Scores		
Machair System						
		F	**p**		***F***	**p**
Area		8.640	**<0.001**		14.189	**<0.001**
Date		1.698	0.193		3.462	0.063
Area*Date		2.599	**0.001**		8.535	**<0.001**
Area	Mean change	***t***	**p**	Mean change	***t***	**p**
Barra	0.014	1.108	0.268	0.026	1.914	0.056
Benbecula	0.024	1.183	0.237	0.035	1.577	0.115
Coll	-0.001	-0.144	0.886	-0.015	-1.614	0.107
Colonsay	0.018	1.642	0.101	-0.032	-2.626	**0.009**
Harris	0.023	1.894	0.058	0.036	2.659	**0.008**
Islay	0.007	0.910	0.363	-0.014	-1.623	0.105
Lewis	0.018	2.155	**0.031**	0.013	1.427	0.154
Monachs	-0.010	-0.646	0.518	0.058	3.517	**<0.001**
North Coast	-0.022	-3.713	**<0.001**	0.024	3.788	**<0.001**
North Uist	-0.007	-1.212	0.226	0.029	4.667	**<0.001**
Sanday	0.000	0.003	0.997	-0.053	-3.906	**<0.001**
Shetland	-0.005	-0.508	0.611	-0.031	-2.751	**0.006**
South Uist	-0.011	-1.739	0.082	0.006	0.883	0.377
Tiree	-0.013	-1.460	0.145	-0.038	-3.864	**<0.001**
Machair Grassland						
		F	**p**		***F***	**p**
Area		3.694	**<0.001**		2.598	**0.004**
Date		9.401	**0.002**		28.997	**<0.001**
Area*Date		7.093	**<0.001**		7.473	**<0.001**
Area	Mean change	*t*	p	Mean change	*t*	p
Barra	0.054	3.279	**0.001**	-0.054	-2.803	**0.005**
Benbecula	0.046	1.537	0.125	-0.003	-0.094	0.925
Coll	-0.023	-1.720	0.086	0.011	0.680	0.497
Colonsay	-0.058	-1.649	0.099	0.033	0.782	0.434
Harris	0.074	3.148	**0.002**	-0.024	-0.857	0.392
Islay	-0.014	-0.780	0.436	0.031	1.438	0.151
Lewis	0.018	1.410	0.159	-0.066	-4.456	**<0.001**
Monachs	0.067	3.519	**<0.001**	0.009	0.404	0.686
North Coast	0.019	1.656	0.098	-0.121	-8.793	**<0.001**
North Uist	0.044	5.329	**<0.001**	-0.035	-3.651	**<0.001**
Sanday	-0.053	-3.243	**0.001**	-0.002	-0.095	0.924
Shetland	-0.026	-1.372	0.170	0.034	1.515	0.130
South Uist	0.014	1.185	0.237	0.003	0.225	0.822
Tiree	-0.044	-3.603	**<0.001**	0.017	1.180	0.238

3.3.2.1 Machair system

Here, only Lewis (+ve) and the North-Coast (-ve) showed a significant shift along Axis 1. Projection of environmental variables suggests a negative shift correlated with increasing acidity and cover of plant species typical of a more acidic heath habitat (Fig. 3.3.a). A positive trend appears to be correlated with an increase in rabbit grazing (Fig. 3.3c). Significant shifts along Axis 2 were more prevalent. Harris, Monachs, N.Coast and N.Uist showed significant positive shifts along Axis 2, correlated with decreasing grazing intensity and cultivation activity, and a corresponding increase in cover of tall grasses (e.g. *Ammophila arenaria*) and bryophytes (Fig. 3.3e). Conversely, Colonsay, Sanday, Shetland and Tiree revealed a negative shift along Axis 2. Here, shifts were shown to correlate with greater grazing intensity, a partial increase in EbN score, and past/recent cultivation activity, along with an increase in associated species.

3.3.2.2 Machair grassland

With the exception of Sanday and Tiree, all significant shifts along Axis 1 were positive, and all significant shifts along Axis 2 were negative. Projection of environmental indicators suggests Axis 1 to be negatively correlated with higher grazing intensity and active cultivation and positively correlated with tall grasses (e.g. *Ammophila arenaria*), while Axis 2 to be negatively correlated with sward heights and plots with no grazing (Fig. 3.3d). This suggests that overall for Barra, Harris, Monachs and N.Uist, grazing intensity and active cultivation have declined since 1976, while Barra, Lewis, N.Coast and N.Uist showed an increase in areas where grazing has ceased. For Sanday and Tiree results suggest an opposing trend, i.e. an increase in land use intensity, through greater grazing pressure, resulting in shorter sward heights of both grasses and forbs (Fig. 3.3d).

3.3.3 Vegetation indicator measures

Significant shifts between surveys were shown between individual components of the CSR strategy scores. The predominant pattern identified was a significant gain in the Competitor component ($p < 0.001$ & $p < 0.001$ for Machair system and grassland respectively) and a concomitant significant fall in the Ruderal component ($p = 0.045$ & $p = 0.005$). As a whole, the functional signature of the vegetation composition (i.e. the balance in proportion of competitor, stress-tolerant and ruderal species) did not change significantly between years for either the Machair system or the Machair grassland, maintaining a balanced C-S-R strategy (Table 3.3).

Comparison of indicator values (IV) scores identified significant changes between surveys for both datasets (Table 3.3). A significant fall in EbL ($p = 0.002$) and EbS ($p = 0.006$) and a significant rise in EbW ($p = 0.024$), EbR ($p = 0.02$) and EbN ($p = 0.024$) were recorded for the Machair system, while for the Machair grassland highly significant rises were found only for EbR ($p < 0.001$) and EbN ($p = 0.008$), and falls for EbW ($p < 0.001$). The latter corresponds well with those species exhibiting the greatest marked decline in percentage cover (Fig. 3.2b), the majority of which are all exclusively wetland species.

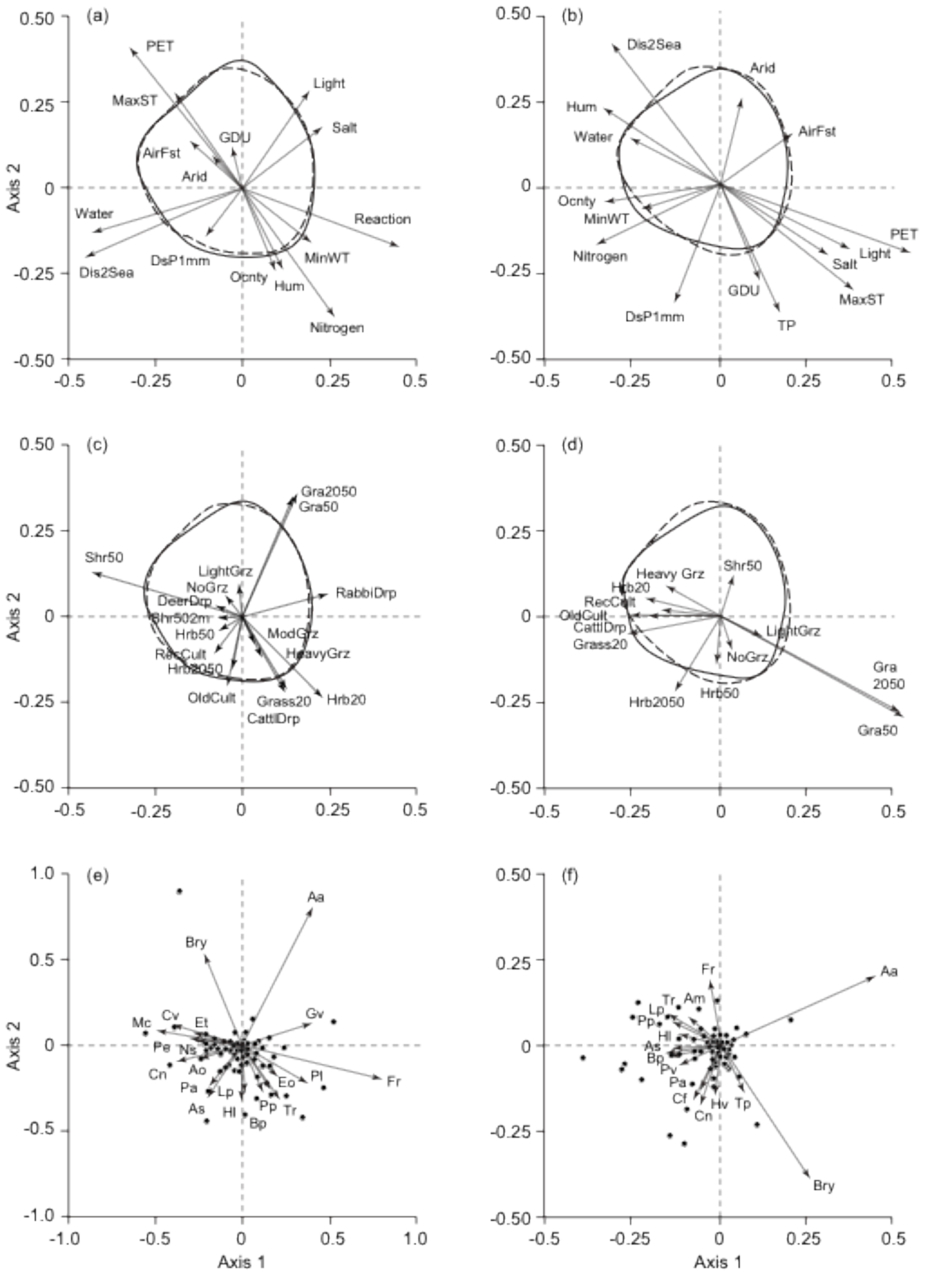


Fig. 3.3 PCA of vegetation composition for the Machair system (a, c & e) and the Machair grassland (b, d & f). Figures: a-d: Displayed are the convex hulls for each survey (dashed and solid lines refer to the survey years 1970 and 2010, respectively), with projected environmental variables p <0.001. Figures: e & f: Displayed as text are species with a significant statistical relationship ($p < 0.001$) and a goodness of fit ($r^2 \geq 0.05$) along Axis 1 and or Axis 2. Species are represented by the following letter codes: As *Agrostis stolonifera*, Aa *Ammophila arenaria*, Ao *Anthoxanthum odoratum,* Am *Achillea millefolium,* Bp *Bellis perenis*, Bry Bryophytes, Cv *Calluna vulgaris*, Cf *Carex flacca*, Cn *Carex nigra*, Et *Erica tetralix*, Eo *Euphrasia officinalis*, Fr *Festuca rubra*, Gv *Galium verum*, Hl *Holcus lanatus*, Hv, *Hydrocotyle vulgaris,* Jg *Juncus geradii*, Lp *Lolium perenne*, Mc *Molinea caerulea*, Ns *Nardus stricta*, Pl *Plantago lanceolata*, Pa *Potentilla anserina*, Pp *Poa pratensis*, Pe *Potentilla erecta*, Pv *Prunella vulgaris*, Tp *Thymus polytrichus,* Tr *Trifolium repens*. Non-significant species are represented by '•'.

REML analysis of the individual CSR components and IV scores at the finer spatial island/area scale revealed significant opposing trends for the areas under study (Figures 3.4 and 3.5).

3.3.3.1 Machair system

Barra, Benbecula, Harris and N.Uist revealed a significant decline in the R-component, with a significant corresponding increase in the C-component (Barra $p = 0.021$; N.Uist $p = 0.028$) and S-component (Benbecula $p = 0.032$; N.Uist $p = 0.014$). This suggests that here, there was less disturbance and an increase in competition for resources in 2010 compared to 1976. Conversely, Colonsay, Islay, Shetland and S.Uist revealed a significant decline in the S-component. Corresponding increases were recorded in the C-component (Islay $p < 0.001$ and S.Uist $p < 0.001$) and in the R component (Colonsay $p = 0.002$ and Shetland $p = 0.043$). Here, results suggest greater disturbance and more plant available resources in 2010 than in 1976 (Fig. 3.4a). Lewis was the only area to show a significant drop in the C-component ($p = 0.013$).

Assessment of IV scores revealed significant changes across 12 of the 14 areas surveyed, with exceptions being Barra and Coll (Fig. 3.5a). The most noteworthy changes were substantial increases in EbN for Islay ($t = 3.015$, $p = 0.003$), Sanday ($t = 9.05$, $p < 0.001$) and Shetland ($t = 5.56$, $p < 0.001$), in EbR for Colonsay ($t = -6.32$, $p < 0.001$) and the N.Coast ($t = -4.75$, $p < 0.001$), decline in EbR for Sanday ($t = 8.72$, $p < 0.001$) and Shetland ($t = 5.59$, $p < 0.001$), and a predominant decline in EbW for Benbecula ($t = -2.24$, $p = 0.025$), Lewis ($t = -3.33$, $p = 0.001$), N.Uist ($t = -4.04$, $p < 0.001$) and Sanday ($t = -1.96$, $p = 0.05$).

Table 3.3 Cover-weighted CSR scores and Ellenberg indicator values for each plot in the Machair system (n=1551) and Machair grassland (n=856). C = competitor score, S = stress score, R = ruderal score, EbL = Ellenberg Light, EbW = Ellenberg Water, EbR = Ellenberg Reaction, EbN = Ellenberg Nutrients, EbS = Ellenberg Salt. Mean plot scores are presented with S.E. in parentheses. Asterisks indicate degree of significance calculated using paired t-tests '***'<0.001, '**'<0.01, '*'< 0.05, 'n.s.'>0.05.

	Machair system			**Machair grassland**		
Year	**1976**	**2010**	**p**	**1976**	**2010**	**p**
C	0.34 (0.003)	0.35 (0.002)	***	0.34 (0.002)	0.35 (0.002)	***
S	0.38 (0.004)	0.38 (0.003)	n.s.	0.36 (0.003)	0.36 (0.004)	n.s.
R	0.27 (0.003)	0.26 (0.003)	*	0.29 (0.003)	0.28 (0.003)	**
EbL	7.60 (0.013)	7.55 (0.011)	**	7.60 (0.017)	7.58 (0.014)	n.s.
EbW	5.46 (0.028)	5.54 (0.024)	**	5.44 (0.038)	5.19 (0.014)	***
EbR	5.69 (0.023)	5.76 (0.020)	*	5.73 (0.027)	5.96 (0.016)	***
EbN	4.05 (0.026)	4.14 (0.024)	*	4.06 (0.034)	4.29 (0.027)	**
EbS	1.03 (0.022)	0.95 (0.018)	**	1.02 (0.029)	1.02 (0.022)	*

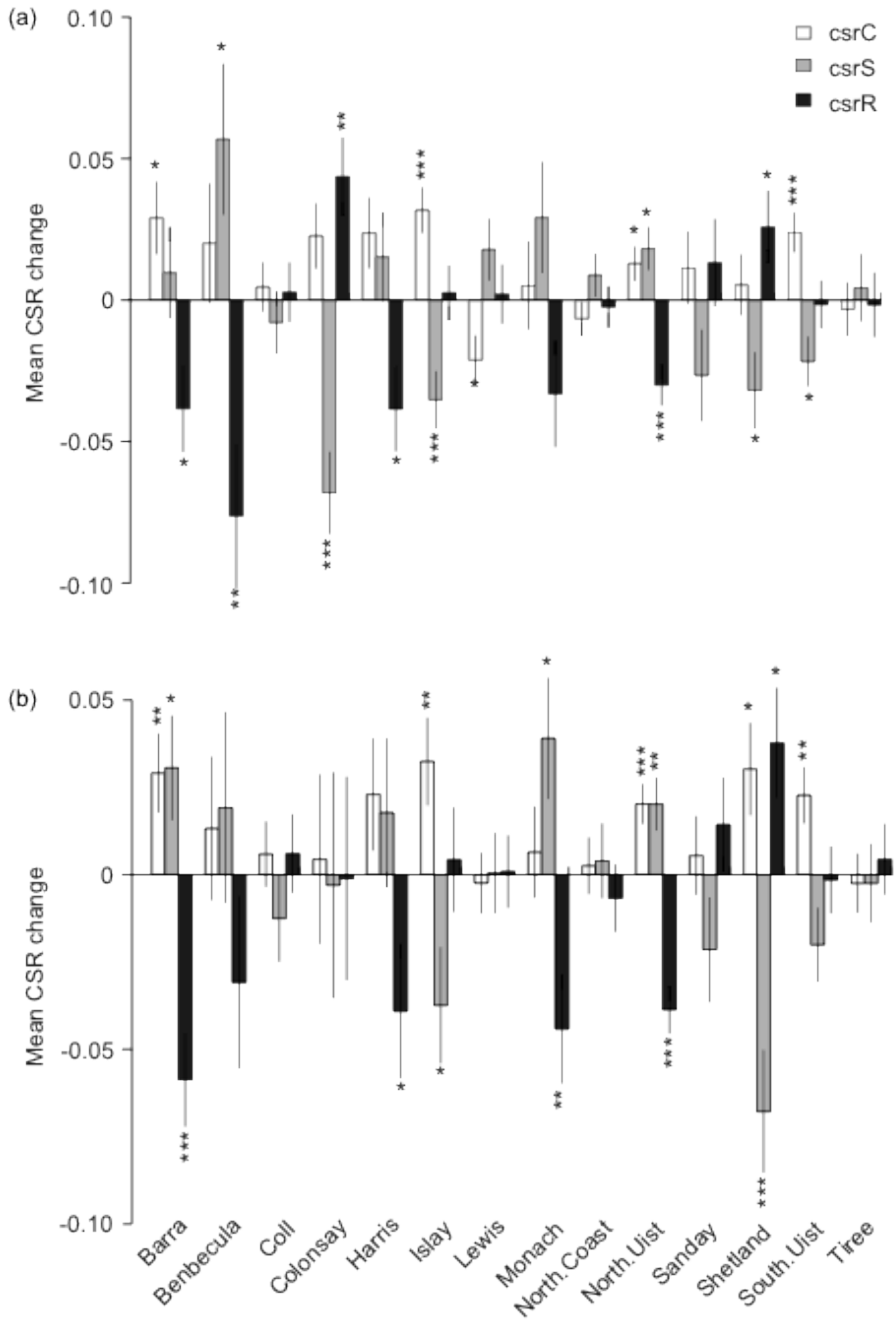


Fig. 3.4 Cover-weighted CSR scores at area/island scale for **(a)** Machair system (n=1551) and **(b)** Machair grassland (n=856). CSR-C = competitor score, CSR-S = stress scores, CSR-R = ruderal score. Mean plot scores are presented with standard error bars of the mean. Asterisks indicate degree of significance calculated with REML analyses '***' <0.001, '**' <0.01, '*'<0.05.

3.3.3.2. Machair grassland

Shifts in the CSR components for the Machair grassland mirrored those patterns for the Machair system, with only a few exceptions (R-component of Colonsay; C-component of the N.Coast; S- & R-components of Tiree). Barra, Monachs, Harris and N.Uist showed a significant fall in the R-component, resulting in a significant corresponding gain in the C-component (Barra $p = 0.009$; N.Uist $p < 0.001$) and S-component (Barra $p = 0.04$; Monachs $p = 0.024$; N.Uist $p = 0.007$). Results suggest that for these areas, there was less disturbance and increased competition for resources in 2010 than 1976. Conversely, Islay and Shetland revealed a significant fall in the S- and gains in the C- (Islay $p = 0.009$ and Shetland $p = 0.021$) and R- (Shetland $p = 0.017$) components. Results suggest here, disturbance and resources were greater in 2010 than 1976 (Fig. 3.4b). S.Uist also showed a marginal decline in the S-component ($p = 0.056$), but the resulting gain in C-component was significant ($p = 0.004$).

Assessment of IV scores revealed significant changes across 11 of 14 areas surveyed, with the exception of Barra, Benbecula and Coll (Fig. 3.5b). The falling trend observed for EbL in the Machair system dataset was mirrored in the Machair grassland sub-set data. However deviations were observed in the remaining four IV scores. The gains in EbN for Islay ($t = 4.04$, $p < 0.001$), Sanday ($t = 9.19$, $p = < 0.001$) and Shetland ($t = 6.34$, $p < 0.001$) remained; significant falls in EbR observed for areas in the Machair system were not found within the Machair grassland. All significant changes in EbW were recorded as a decline.

3.3.4 Condition indicators of Machair quality

Species indicative of good and poor quality Machair, fallowed land and active cultivation were found to divide the areas under study between those where richness of the indicators increased (Barra, Coll, Colonsay, Islay, S.Uist and Tiree) and those where it declined (Benbecula, Harris, Lewis, Monachs, N.Coast, N.Uist, Sanday and Shetland; Fig. 3.6a). Results suggest the changes on Benbecula, Monachs and Shetland to be of particular concern, indicating a significant decline in species (number and cover) seen as typical of good quality Machair (Fig. 3.6b).

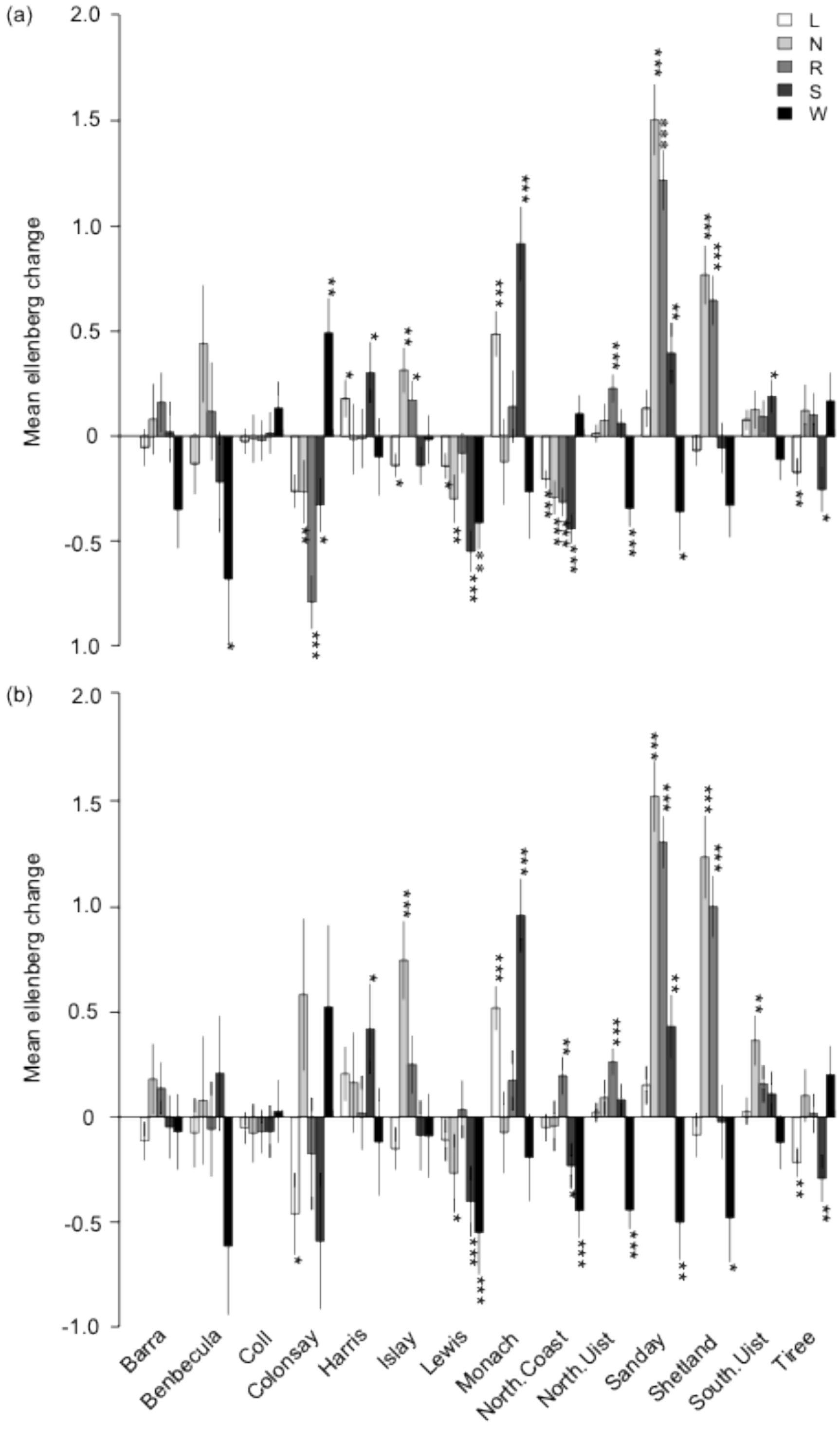


Fig. 3.5 Ellenberg indicator values at the area/island scale for: **(a)** Machair system (n=1551) and **(b)** Machair grassland (n=856). L = Light, N = Nitrogen, R = Reaction, S = Salt, W = Water. Mean plot scores are presented with standard error bars of the mean. Asterisks indicate degree of significance calculated with REML analyses '***'<0.001, '**'<0.01, '*'<0.05.

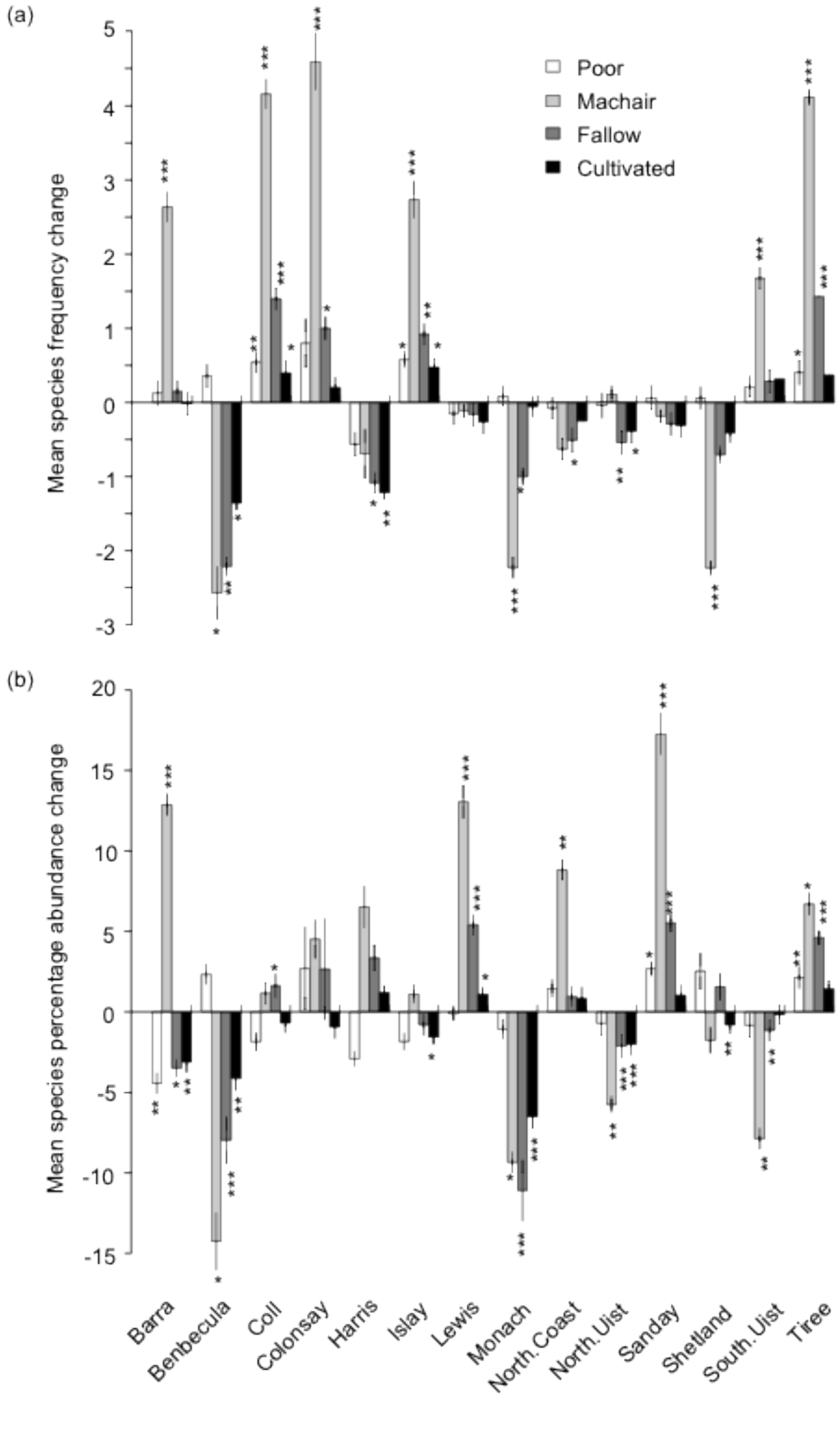


Fig. 3.6 (a) Mean frequency and **(b)** %-cover change for species groups indicative of different Machair quality. Analyses at area/island scale for Machair grassland only (n=856). Mean frequency differences are presented with standard error bars of the mean. Asterisks indicate the degree of significance calculated with GLMM (Frequency) and REML (% Cover) analyses '***'<0.001, '**'<0.01, '*'<0.05.

3.4 Discussion

Semi-natural vegetation can show substantial resistance to external drivers of change, particularly where communities are dominated by slow-growing, stress-tolerant species (Grime et al. 2008). Resistance of vegetation communities to the changing environment, coupled with the scarcity of historic data and inconsistencies in the quality of long-term datasets (Thomas et al. 2004b), can limit understanding of how vegetation responds to shifts in the external environment even in moderate scale monitoring studies. However, where such data exist, there is the potential to add to the understanding of ecological responses to environmental and socio-economic change. The surveys reported here have particular value because they are sampled in a statistically-rigorous manner, covering almost the entire Machair resource at the national scale. This resource and its component grasslands have both a high conservation interest at the national scale, and a high cultural value at the local scale. The results derived here can therefore, be used by policy-makers with some degree of confidence.

3.4.1 Species compositional change

The overall rise in species diversity within the Machair system and Machair grassland suggests a change in species community dynamics through time. This pattern is most evident for the areas of Barra, Coll, Colonsay, Islay, S.Uist and Tiree; here, a large proportion of those species within the Machair grassland were indicative of good quality Machair (Fig. 3.6a). The botanical diversity and conservation value of the Machair is usually attributed to the traditional land management regimes (Angus 1996; Crawford 1990, 1997; Owen et al. 2000), i.e. rotational cultivation involving traditional methods of cultivated strips of land and areas left as fallow. At the time of the repeat survey, this practice was virtually confined to the Uists, specifically the North, South and Benbecula (Angus 2009; Pakeman et al. 2011). Many of the other islands are farmed rather than crofted. Therefore, for Barra, Coll, Colonsay, Islay and Tiree, observed increases in species indicative of Machair and species-rich fallow imply active management of the Machair systems may to be more in line with conservation objectives today than in 1976.

Patterns observed in this study may have resulted from designations of Environmentally Sensitive Areas (ESA) encompassing much of the Machair resource. Introduced to Scotland, in 1987, ESA schemes provided financial incentives to farmers, crofters and common grazing committees to undertake environmentally friendly practices to maintain and enhance biodiversity, landscape and historic values of designated habitats. The schemes have since been superseded by other agri-environment schemes, but their application may have started a process of engagement with altering agricultural practices to safeguard and enhance areas of conservation and national heritage importance. Results suggest a clear correlation between several Machair areas designated under the ESA scheme (Barra, Coll, Colonsay, Islay, North and South Uist, and Tiree, Roberts et al. 2002) and reported increases in species indicative of Machair grasslands and rotational arable agriculture. This suggests for those regions where traditional, low-intensity rotational arable agriculture was incentivised; the floristic diversity of the Machairs has flourished (Fig. 3.7), in comparison to areas without government support to manage in an environmentally sensitive manner.

There are however exceptions to this pattern, as the more northern ESA designated areas Benbecula, North Uist and Shetland, displayed significant declines in species indicative of Machair, and rotational arable agriculture, suggesting for these regions a decline in biodiversity value of Machair grasslands. With the exception of Shetland, these regions, along with Harris and Monachs were shown to display declines in the CSR-R component and a corresponding gain in the CSR-C component. This pattern probably reflects an overall decline in active management, particularly in grazing intensity (Pakeman et al. 2011). A reduction in grazing pressure will often give rise to increased dominance of competitor species, reducing the community diversity as competition for space, light and nutrients increases (Pakeman 2004). Results here raise concern over the current and future condition of the Machair, particularly of N.Uist and Benbecula.

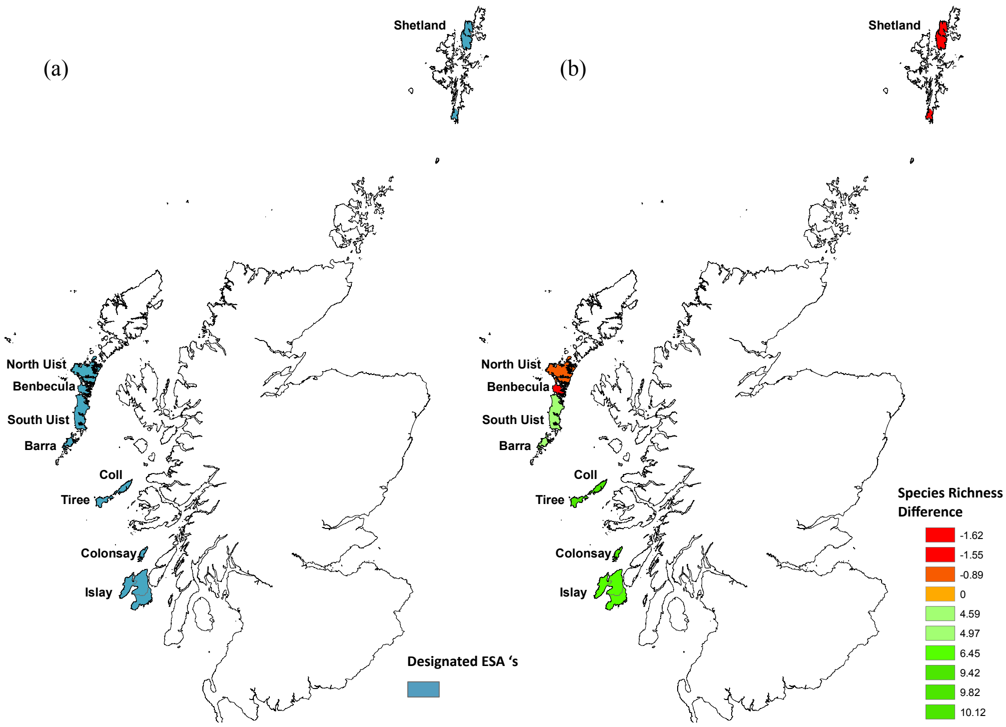


Fig. 3.7 (a) Surveyed regions once designated as an Environmentally Sensitive Area (ESA); **(b)** Biodiversity gains and loss since 1976 for ESA designated regions.

Patterns reported for the Shetland isles differed in that the CSR-R component increased, while the CSR-S component decreased, notably so among the Machair grasslands, suggesting a significant increase in disturbance. Alongside a significant increase in Ellenberg Indicator values for nitrogen (EbN), it is suggestive of agricultural intensification. Ordinations identified a positive association between EbN and areas subject to heavy grazing and cultivation resulting in short grassy swards. Therefore the rise in EbN and subsequent decline in CSR-S may be a result of either increased stocking densities of cattle or through the direct application of artificial fertilisers. Agricultural census data, suggest Shetland reported a 31% increase in cattle density over the survey period, contrary to most other regions where declines were recorded (Pakeman et al. 2011). Further, Pakeman et al. (2011) describe an overall trend in the increased use of inorganic fertilisers, and despite funding incentives (Angus 2009), a reduction in the application of kelp (*Laminaria hyperborea)* as organic fertiliser across much of the Scottish Machair resource. A shift away from organic fertiliser could have serious implications for the Machair, not least through impacting the weed and fallow species for these areas and ultimately the species that depend on them (Redpath et al. 2010), but also through long-term issues concerning stabilisation, as seaweed acts as a soil binding agent and reduces the risk of sand-blow (Kerr 1954). Machair soils are well described in Glentworth (1979) and Hudson (1991) but typically consist of a poorly developed 'A' horizon overlying calcareous shell-sand substrata. Therefore a reduction in the application of additional organic matter can result in the destabilisation of this 'A' horizon, increasing vulnerability of the Machairs to widespread sand-blow.

It is possible that the effects of destabilisation are already being witnessed. *Leymus arenarius*, a tall herbaceous N–demanding species (Hill et al. 1999) extremely tolerant of sand burial was reported here to increase substantially in terms of percentage cover, particularly among the Machair grasslands. Destabilisation of the Machair grasslands will significantly impact on their biodiversity, and is of particular concern, given future climatic scenarios of increased prevalence of high winds and storms for the western isles of Scotland (Hansom and Angus 2001; Jenkins et al. 2003).

However, patterns observed in the CSR-S scores and EbN values for Shetland were also observed for several machair regions displaying increased biodiversity, including a rise in species typical of Machair and fallow areas. The pattern was most evident for Colonsay, Islay and S.Uist. It is possible that moderate fertiliser application, in conjunction with low-intensity arable farming promotes biodiversity, as disturbance and increased nutrients reduce the competitive interaction between species allowing more species from regional species pools to coexist (Mayfield et al. 2010); this is in line with the intermediate disturbance hypothesis (IDH; Grime 1973; Connell and Slatyer 1977; Connell 1978). Indeed, a monitoring assessment of ESA areas of the Uists in 1998 (Nolan et al. 1998) reported that the species biodiversity of Machair grasslands were being maintained, despite findings of higher levels of topsoil nitrogen. However, where disturbance may be in decline, competitive species are less constrained. Here, increased biodiversity may be observed due to high nutrient availability, at the expense of increased dominance of rank vegetation, suppressing the overall cover of species of conservation importance. Only in S. Uist, a region highlighted by Angus (1996) as representing some of the best examples of Hebridean Machair, was the pattern of increased species richness, yet decreased abundance, observed.

Changes in species richness and diversity indices have also been linked to increasing community similarity (biotic homogenisation); previously distinct plant communities containing more specialised species, become progressively similar as they are replaced by more widespread generalists (McKinney and Lockwood, 1999, Smart et al. 2006). Biotic homogenisation was noted on Lewis in particular, where the degree of within-community similarity in the re-survey was greater than in the original survey and, as a result a decline in compositional distance between plots was observed. Furthermore a decline in species indicative of high-quality Machair and traditional land use were reported on Lewis, while the cover of remaining species increased significantly. This pattern conforms to the results of Smart et al. (2006), where land use changes prompted a decline in sub-ordinate species, allowing remaining species to increase and characterise the vegetation with little invasion of new dominants. This pattern was most pronounced for the Isle of Lewis but was also observed for Harris, N.Coast, Sanday and to a lesser extent Shetland.

The most widespread change in vegetation composition measures was the decrease in the Ellenberg-W value at most areas/islands under study. Results were consistent with the declines in cover of *Alopecurus geniculatus, Carex rostrata, Menyanthes trifoliata, Myrica gale* and *Petasites hybridus* within the Machair system, and *Eleocharis uniglumis, Equisetum palustre* and *Iris pseudacorus* within the Machair grassland. *Phragmites australis*, declined substantially in both datasets. All these species are wetland specialists, suggesting a substantial drying out of the Machair systems and grasslands between surveys. These results diverge from the widespread increase in Ellenberg-W reported across Scotland (Norton et al. 2009) in the most recent of the Countryside Surveys of 2007 (Carey et al. 2008) in which changes in the entire vegetation resource within Great Britain and the Islands are monitored over successive years at permanent plots located randomly over 1 km^2 units. The Regional Climate Model (RCM) commissioned by the British-Irish Council (BIC) anticipates an increase in winter precipitation of up to 8% for the Western Isles of Scotland, with an even greater increase further north (Jenkins et al. 2003). Furthermore, according to Angus and Hansom (2004), there is already a perception on the Western Isles that seasonal winter water covers a greater extent on the Machair than in previous years, prolonging flooding and potentially inhibiting ploughing of arable Machair; however, this is not borne out by the vegetation data reported here.

3.5 Conclusions

Machair is not a natural habitat *per se*, but rather has developed in tandem with human settlement over the last three centuries. Its biodiversity value is acknowledged to be dependent on the active management of rotational cultivation and grazing regimes (Angus 2001). However, maintaining biodiversity in a favourable condition with pressures of socio-economic and environmental change is not straightforward. Results of this study provide clear evidence for change in biodiversity for many of the Scottish regions that support this rare biotype, and through the investigation of shifts in functional strategies, much of the observed change can be reasonably well linked to reported shifts in land use management.

Scotland has a special responsibility for the conservation and maintenance of these internationally important areas of cultural and biodiversity importance. Results reported here support the views and opinions of the crofting and farming populations (Pakeman et al. 2011), identifying concerns linked to use of artificial fertiliser and agricultural intensification, or conversely a reduction in grazing intensity and agricultural practices. There is also anecdotal evidence that the Machair is becoming drier and less stable which clearly warrants further research. Nevertheless, biodiversity was identified to increase for several regions, potentially linked to past government incentivised schemes. This study clearly identifies significant regional differences in the current condition of the Machair and also differences in the potential causes and direction of future change. This emphasises the need for regional-scale and arguable finer assessment of the Machair for the successful implementation of conservation management, as national conservation management plans are unlikely to address individual requirements specific to different regions. It also stresses the importance and necessity of fine resolution long-term monitoring in understanding ecological responses, particularly of ecosystems vulnerable to multiple drivers of biodiversity change.

REFERENCES

Angus, S. 1994. The conservation importance of the Machair systems of the Scottish islands, with particular reference to the Outer Hebrides. Usher, M.B. and Baxter, J. (Ed.). The Islands of Scotland: a Living Marine Heritage, 95-120. HMSO, Edinburgh.

Angus, S. 1996. Natural heritage conservation in the Southern Outer Hebrides. In: Gilbertson, D., Kent, M. and Grattan, J. (eds.) The Outer Hebrides: the last 14,000 years, pp. 227- 250. Sheffield Academic Press, Sheffield.

Angus, S. 2001. The Outer Hebrides: moor and machair. White Horse Press, Harris and Cambridge.

Angus, S. 2006. De tha Machair? Towards a Machair definition. Sand dune Machair 4, 7-22. Aberdeen Institute for Coastal Science and Management, Aberdeen.

Angus, S. 2009. Dé tha cearr air a'mhachaire? Biodiversity issues for Scottish Machair: an initial appraisal. The Glasgow Naturalist, 25, Supplement. Machair Conservation: Successes and Challenges, 53-62.

Angus, S. and Dargie, T. 2002. The UK Machair habitat action plan: progress and problems. Botanical Journal of Scotland 54, 63-74.

Angus, S. and Hansom, J.D. 2004. Tir a' Mhachair, Tir nan Loch? Climate change scenarios for Scottish Machair Systems: A wet future? Proceedings Vol.2. Littoral 2004. Delivering sustainable coast: connecting science and policy. 565-569.

Anon. 2008. UK biodiversity action plan priority habitat descriptions: Machair. JNCC. Peterborough.

Bennie, J., Hill, M.O., Baxter, R. and Huntley, B. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. Journal of Ecology 94, 335-368.

Caird, J.B. 1979. Land use in the Uists since 1800. Proceedings of the Royal Society of Edinburgh, 77B, 505-527.

Carey, P.D., Wallis, S., Chamberlain, P.M., Cooper, A., Emmett, B.A. et al. 2008. Countryside Survey: UK Results from 2007. NERC/Centre for Ecology and Hydrology, 105pp. (CEH Project Number: C03259).

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M. et al. 2000. Consequences of changing biodiversity. Nature. 405, 234-242.

Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111, 1119-1144.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Corney, P.M., Le Duc, M.G., Smart, S.M., Kirby, K.J., Bunce, R.G.H. and Marrs, R.H. 2006. Relationship between the species composition of the forest field layer vegetation and environmental drivers, assessed using a national scale survey. Journal of Ecology 94, 383-401.

Crawford, I.C. 1990. Agriculture, weeds and the Western Isles Machair. Transactions of the Botanical society of Edinburgh 45, 483-492.

Crawford, I.C. 1997. The conservation and management of Machair. Botanical Journal of Scotland 49, 433-439.

Ellenberg, H. 1988. Vegetation ecology of Central Europe. 4th ed. Cambridge University Press, Cambridge, UK.

Ellis, C.J. and Coppins, B.J. 2007. Reproductive strategy and the compositional dynamics of crustose lichen communities on aspen (Populus tremula L.) in Scotland. The Lichenologist 39, 377-391.

Glentworth, R. 1979. Observations on the soils of the Outer Hebrides. Proceedings of the Royal Society of Edinburgh. Section B-Biological Sciences 77, 123-137.

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

Grime, J.P. 1974. Vegetation classification by reference to strategies. Nature 250, 26-31

Grime, J.P., Hodgson, J.G. and Hunt, R. 1988. Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London.

Grime, J.P., Fridley, J.D., Askew, A.P., Thompson, K., Hodgson, J.G. and Bennet, C.R. 2008. Long term resistance to simulated climate change in an infertile grassland. Proceedings of the National Academy of Sciences 105, 10028-10032.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.E. and Knight, M.E. 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

Hagreaves, G.H. and Samani, Z.A. 1985. Reference crop evapotranspiration from temperature. Applied Engineering in Agriculture 2, 96-99.

Hansom, J.D. and Angus, S. 2001. "Tir a' Mhachair (land of the machair): sediment supply and climate change scenarios for the future of the Outer Hebrides machair". In Earth Science and the Natural Heritage of Scotland, Edited by: Gordon, J.E. 68–81. The Stationery Office.

Hill, M.O. 1993. TABLEFIT, Version 1.0 for Identification of vegetation types. Institute of Terrestrial Ecology, Huntingdon.

Hill, M.O., Mountford, J.O., Roy, D.B. and Bunce, R.G.H. 1999. Ellenberg indicator values for British plants, ECOFACT, vol 2, technical annex. ITE Monkswood, Huntingdon, Department of the Environment, Transport and the Regions, London, UK.

Hudson, G. 1991. Geomorphology and soils of the Outer Hebrides', In Pankhurst, R.J. and Mullin, J.M. (eds) Flora of the Outer Hebrides, 19–27. London: Natural History Museum.

Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnet, N.P. et al. 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. Applied Vegetation Science 7, 163-170.

IPCC. 2007. Climate change. 2007. The physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L., (Eds), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 996.

Jenkins, G., Cooper, C., Hassell, D. and Jones, R. 2003. Scenarios for climate change for islands within the BIC region. Produced for the British-Irish Council by the Meteorological Office, Bracknell.

Jenkins, G.J., Perry, M.C. and Prior, M.J.O. 2007. The climate of the United Kingdom and recent trends. Met Office Hadley Centre, Exeter.

Joint Nature Conservation Committee (JNCC). 2004. Common standards monitoring guidance for sand dune habitats. <jncc.defra.gov.uk> (accessed 19.01.12).

Kent, D.H. 1992. List of vascular plants of the British Isles. Botanical Society of the British Isles, London.

Kerr, D.H. 1954. Machair land in the Outer Isles. Scottish Agriculture 34, 157-161.

Legendre, P. and Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

Mackenzie, A.F.D. 2007. The contribution of crofting in the 21st Century. Committee of Inquiry on Crofting. < www.croftingenquiry.org> (accessed 19.01.2012).

Marrs, R.H. Le Duc, M.G., Smart, S.M., Kirby, K.J, Bunce, R.G.H. and Corney, P.M. 2011. Aliens or natives: who are the 'thugs' in British woods? Kew Bulletin 65, 583-594.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. and Vesk, P.A. 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land use change. Global Ecology and Biogeography 19, 423-431.

McCollin, D., Moore, L. and Sparks, T. 2000. The flora of a cultural landscape: environmental determinants of change revealed using archival sources. Biological Conservation 92**,** 249-263.

McGovern, S., Evans, C.D., Dennis, P., Walmsley, C. and McDonald, M.A. 2011. Identifying drivers of species compositional change in a semi-natural upland grassland over a 40-year period. Journal of Vegetation Science 22, 346-356.

McKinney, M.L. and Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14, 450-453.

McMaster, G.S. and Wilhelm, W.W. 1997. Growing degree-days: one equation, two interpretations. Agricultural and Forest Meteorology 87, 291-300.

Nolan, A.J., Henderson, D.J., Bell, S.J. and Gauld, J.H. 1998. The Environmentally Sensitive Areas designated in Scotland: The machair of the Uists and Benbecula, Barra and Vatersay ESA monitoring report. Macaulay Land Use Research Institute, Scotland.

Norton, L.R., Murphy, J., Reynolds, B., Marks, S. and Mackey, E.C. 2009. Countryside Survey: Scotland Results from 2007. NERC/Centre for Ecology and Hydrology, The Scottish Government, Scottish Natural Heritage, 83pp. (CEH Project Number: C03259).

Oksanen, J., Kindt, R., Legendre, P., O'Hara, R.B. et al. 2009. vegan: community ecology package. R package version 1.9-25. (http://cran.r-project.org/).

Owen, N.W., Kent, M. and Dale, P. 1996. The Machair vegetation of the Outer Hebrides: a review. In Gilberson, D., Kent, M. and Gratton, J. (eds), The Outer Hebrides: the last 14000 years. Sheffield University Press, Sheffield. pp. 123-131.

Owen, N.W., Kent, M. and Dale, P. 2000. Ecological effects of cultivation on the Machair sand dune systems of the Outer Hebrides, Scotland. Journal of Coastal Conservation 6, 155-170.

Pakeman, R.J. 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. Journal or Ecology 92, 893-905.

Pakeman, R.J., Huband, S., Kriel, A. and Lewis, R.J. 2011. Changes in the management of Scottish Machair communities and associated habitats from the 1970s to the present. Scottish Geographical Journal 127, 267-287.

Parmesan, C and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 42, 37-42.

Perry, M. and Hollis, D. 2005. The development of a new set of long-term climate averages for the United Kingdom. International Journal of Climatology 25, 1023-1039.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and the R Development Core Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-102.

R Development Core Team 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Redpath, N., Osgathorpe, L.M., Park, K. and Goulson, D. 2010. Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland. Biological Conservation 143, 492-500.

Ritchie, W. 1976. The meaning and definition of machair. Transactions of the Botanical Society of Edinburgh 42**,** 431-440.

Roberts, D., Macdonald, D, Kampas, T., Shannon, P., Potts, J. et al. 2002. Nature conservation designations and land values. Macaulay Land use Research Institute. Scotland.

Rodwell, J.S. 1991a. British plant communities. Volume 1: Woodlands and scrub. University Press Cambridge.

Rodwell, J.S. 1991b. British plant communities. Volume 2: Mires and heaths. University Press Cambridge.

Rodwell, J.S. 1992. British plant communities. Volume 3: Grasslands and montane communities. University Press Cambridge.

Rodwell, J.S. 2000. British plant communities. Volume 5: Maritime communities and vegetation of open habitats. University Press Cambridge.

Ross, L.C., Woodin, S.J., Hester, A., Thompson, D.B.A and Birks, H.J.B. 2010. How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? Plant Ecology and Diversity 3, 1-8.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfied, J. et al. 2000. Biodiversity – global biodiversity scenarios for the year 2100. Science 287, 1770-1774.

Shaw, M.W., Hewett, D.G. and Pizzey, J.M. 1983. Scottish Coastal Survey. Institute of Terrestrial Ecology. Bangor Research Station, Bangor, Gwynedd.

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C. and Firbank, L.G. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. Proceedings of the Royal Society B-Biological Sciences 273, 2659-2665.

Stace, C. 2010. New flora of the British Isles. Cambridge University Press, Cambridge, UK.

Thomas, C.D., Cameron, A., Green, R.E., Bakkeness, M., Beaumont, L.J. et al. 2004a. Extinction risk from climate change. Nature 427, 145-148.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D. et al. 2004b. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303**,** 1879-1881.

Thornthwaite, C.W. 1948. An approach towards a rational classification of climate. Geographical Review 38, 55-94.

Appendix 3.0

Appendix 3.1 Site Information and climate data for each of the sites used in the analysis.

ID	Site Location	Site Name	Plots	East	North	Annual Mean Temp (°C)		Precipitation (mm yr^{-1})		Growing Degree Units		Potential Evapo-transpiration (mm d^{-1})		Aridity		Monthly Mean Humidity (%)	
						1961-77	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*
3	Islay	Laggan	34	130	654	9.0	9.4	1195	1355	1250.3	1416.1	63.7	62.3	0.66	0.66	84.0	83.2
4	Islay	Machir Bay	29	121	663	8.3	8.8	1141	1376	1079.2	1203.1	56.7	55.8	0.65	0.62	84.3	83.5
5	Islay	Saligo bay	25	121	666	8.9	9.4	1102	1321	1232.0	1374.4	59.1	58.3	0.67	0.64	84.1	83.2
6	Islay	Gruinart	53	130	673	9.0	9.5	1181	1401	1275.9	1438.8	61.9	61.0	0.66	0.64	83.2	82.2
7	Colonsay	Oronsay	33	135	688	9.0	9.7	1128	1206	1374.1	1513.6	61.5	59.8	0.66	0.66	83.5	82.2
8	Colonsay	Garvard	19	135	691	9.0	9.7	1128	1208	1363.4	1503.9	61.5	59.8	0.66	0.66	83.5	82.3
9	Colonsay	Kiloran	18	140	697	9.2	9.8	1171	1240	1385.8	1536.7	62.3	60.7	0.65	0.66	83.6	82.2
12	Tiree	West Tiree	54	094	743	9.0	9.6	1056	1232	1279.9	1407.1	55.0	55.1	0.64	0.64	85.2	82.9
13	Tiree	North Tiree	27	096	747	9.0	9.5	1089	1259	1267.8	1399.4	55.6	55.7	0.64	0.63	85.1	82.8
14	Tiree	Crossapoll	22	099	743	8.9	9.5	1063	1232	1257.8	1388.8	55.6	55.6	0.64	0.63	85.1	82.8
15	Coll	West Coll	61	113	753	9.0	9.5	1099	1272	1285.2	1409.7	55.8	55.9	0.64	0.64	84.8	82.4
16	Coll	Clabhach	26	117	756	8.8	9.4	1175	1432	1250.2	1379.0	55.9	55.6	0.63	0.61	84.8	82.5
17	Coll	Gallawach	32	121	761	8.9	9.5	1302	1579	1296.5	1417.1	56.4	56.0	0.59	0.59	84.6	82.3
18	Barra	Vatersay	20	063	795	8.9	9.6	1270	1241	1336.7	1446.3	52.1	52.1	0.63	0.63	86.3	84.1
19	Barra	West Barra	9	064	801	8.7	9.4	1412	1332	1283.0	1388.4	50.3	50.3	0.60	0.61	86.4	84.1
20	Barra	N Barra	27	069	806	8.9	9.6	1535	1388	1335.2	1446.6	52.2	52.3	0.58	0.61	86.5	84.1
21	South Uist	Daliburgh	48	073	822	8.8	9.4	1363	1364	1220.7	1363.9	54.7	54.3	0.61	0.63	86.5	83.9
22	South Uist	Ormiclate	31	073	830	8.8	9.4	1337	1404	1213.6	1354.4	54.0	53.8	0.60	0.62	86.4	83.7
23	South Uist	Howbeg	16	074	835	8.7	9.3	1305	1398	1178.2	1334.8	54.3	53.8	0.61	0.62	86.7	83.9
24	South Uist	N.Stiligarry	23	075	840	8.6	9.3	1278	1308	1178.9	1328.6	53.9	53.8	0.61	0.64	86.8	83.9
25	South Uist	Loch Bee	46	075	844	8.6	9.3	1256	1307	1179.7	1329.5	53.9	53.8	0.62	0.64	86.7	83.8
26	Benbecula	Borve	20	077	850	8.6	9.3	1168	1280	1178.7	1334.2	54.4	54.3	0.64	0.64	86.2	83.2
27	South Uist	S.Stilligarry	29	075	837	8.6	9.2	1297	1409	1160.4	1321.5	54.6	54.0	0.61	0.62	86.7	83.9
28	North Uist	Baleshare	50	078	860	8.6	9.2	1118	1254	1181.2	1356.4	57.2	56.5	0.66	0.66	85.9	82.8
29	North Uist	Kirkibost	13	075	864	8.5	9.2	1098	1257	1164.7	1349.2	58.0	56.9	0.66	0.65	86.1	83.0
30	Monach	Monach Isles	37	063	862												
31	North Uist	Paible	11	072	867	8.6	9.2	1080	1274	1169.9	1317.5	53.8	53.3	0.65	0.63	86.2	83.2
32	North Uist	Hosta	22	071	873	8.6	9.2	1079	1306	1163.5	1299.2	52.6	52.1	0.64	0.62	86.3	83.3
33	North Uist	Vallay	27	077	876	8.5	9.1	1132	1349	1153.9	1312.0	55.8	54.8	0.64	0.62	86.4	83.4
34	North Uist	Leathann	30	081	876	8.6	9.2	1091	1328	1182.5	1329.9	55.7	54.9	0.65	0.63	86.5	83.5
35	North Uist	Balranald	23	070	869	8.6	9.2	1080	1286	1168.6	1311.9	53.5	53.1	0.64	0.62	86.3	83.2
36	North Uist	Robach	26	087	876	8.6	9.2	1083	1326	1193.8	1328.3	55.4	54.9	0.65	0.62	86.4	83.4
37	North Uist	Berneray	57	090	882	8.6	9.2	1083	1393	1201.2	1281.7	51.3	51.8	0.63	0.60	86.7	83.7
39	Harris	Northton	31	098	891	6.9	7.5	1219	1678	819.9	830.9	43.1	44.1	0.55	0.52	87.0	83.9
40	Harris	Luskintyre	27	106	898	8.5	9.2	1619	1890	1199.4	1316.9	58.7	57.8	0.55	0.55	86.7	83.7

Appendix 3.1 Continued..

ID	Site Location	Site Name	Plots	East	North	Annual Mean Temp (°C)		Precipitation (mm yr^{-1})		Growing Degree Units		Potential Evapo-transpiration (mm d^{-1})		Aridity		Monthly Mean Humidity (%)	
						1961-77	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*
41	Lewis	Uig	24	103	932	8.2	9.0	1329	1635	1169.2	1274.5	52.7	51.6	0.62	0.60	87.0	83.7
42	Lewis	Valtos	19	109	936	8.4	9.2	1432	1659	1236.5	1338.2	54.4	53.5	0.60	0.60	86.9	83.5
43	Lewis	Barvas	27	135	951	7.9	8.5	1192	1415	1038.6	1189.4	56.8	54.6	0.64	0.63	87.0	83.6
44	Lewis	Tolsta	25	154	948	7.4	8.1	1175	1419	917.3	1062.9	54.7	52.2	0.64	0.62	87.4	83.9
45	Lewis	Tolsta	25	154	948	7.4	8.1	1175	1419	917.3	1062.9	54.7	52.2	0.64	0.62	87.4	83.9
47	Shetland	Quendale	30	438	111	7.8	8.4	995	1027	927.1	1070.8	46.4	45.8	0.68	0.69	84.9	82.3
48	Shetland	Scousburgh	25	437	111	7.7	8.3	1063	1087	899.6	1046.6	46.1	45.3	0.67	0.68	85.3	82.7
49	Shetland	Breckon	25	453	120	7.1	7.8	1135	1107	851.2	993.9	50.7	50.3	0.66	0.68	86.2	83.0
51	Orkney	Holland	27	363	103	7.7	8.3	938	994	919.6	1049.1	47.6	48.3	0.67	0.69	86.4	84.8
53	North Coast	Oldshore More	27	220	958	7.9	8.5	1136	1386	1036.6	1224.2	59.1	59.2	0.66	0.67	85.6	83.4
54	North Coast	Sheigra	24	218	960	8.1	8.7	1071	1357	1057.7	1214.1	53.1	53.8	0.64	0.64	86.0	83.9
55	North Coast	Durness	23	237	967	7.7	8.4	1281	1481	947.7	1174.3	57.9	57.5	0.63	0.63	85.6	83.6
56	North Coast	Faraid Head	24	239	970	7.8	8.5	1320	1531	980.7	1197.2	56.8	56.4	0.61	0.61	85.7	83.6
57	North Coast	Bettyhill	27	269	961	7.9	8.5	926	1037	1080.1	1223.1	60.2	60.8	0.70	0.71	85.2	83.2
58	North Coast	Farr Bay	24	271	962	7.6	8.2	856	993	1025.1	1156.8	59.9	60.3	0.72	0.72	85.2	83.1
59	North Coast	Strathy	20	283	965	7.8	8.3	868	957	969.8	1085.0	56.7	57.2	0.70	0.70	85.4	83.4
60	North Coast	Melvich	18	288	964	7.3	7.8	961	1060	919.2	1055.9	60.7	60.8	0.70	0.69	84.6	82.7
61	North Coast	Reay	22	296	965	8.1	8.7	899	932	1077.2	1248.7	61.8	62.3	0.71	0.73	84.7	83.0
62	North Coast	Dunnet	23	322	969	7.5	8.1	840	995	939.4	1091.7	62.2	62.3	0.73	0.71	84.6	83.4
64	North Coast	Sandwood	20	221	964	7.4	8.1	1146	1426	910.5	1087.8	55.5	55.5	0.64	0.63	85.8	83.7
73	Orkney	Overbister	28	370	104	7.9	8.5	933	964	959.3	1094.6	48.4	49.0	0.67	0.71	86.4	84.7

N.B. No climate data available for the Monach Isles.

Supplementary Material (S3)

Table S3.1 Environmental variables used in the ordination analyses of the Machair System and Machair grassland between years. The number and type of variables used in the analysis and their abbreviations are presented. **V** refers to variable type: b. binary; c. continuous; f. factorial; o. ordinal. **N** refers to the number of variables per group

Variable group	V	N	Data description	Variables used in the analysis	Abbreviation
Climate	c	10	UK Met Office 5km monthly gridded climatic data and climate indices. Long-term averages 1961-1977 & 1990 - 2006	Minimum winter temperature ($^{\circ}$C)	MinWT
				Maximum summer temperature ($^{\circ}$C)	MaxST
				Total precipitation (mm)	TP
				Days of precipitation >1mm	DsP1mm
				Days of air frost (d^{-1year})	AirFst
				Humidity ($\%^{avgpcm}$)	Hum
				Potential evapotranspiration (mm^{d-1})	PET
				Aridity	Arid
				Oceanicity	Ocnty
				Growing degree units ($^{GDU's}$)	GDU
Animal signs	b	5	Plot level presence or absence of dung from 5 herbivore species	Cattle	N/A
				Sheep	N/A
				Rabbits	N/A
				Deer	N/A
				Horse	N/A
Grazing pressure	f	4	Intensity of herbivore grazing pressure	None	NoGrz
				Light	LghtGrz
				Moderate	ModGrz
				Heavy	HvyGrz
Vegetation structure	o	6	Indication of vegetation height and structure for each plot (0,1,2,3 = no, sparse, intermediate and full cover respectively). Three height categories for grasses and herbs. Shrubs have different scaled categories.	< 20cm	Struc<20cm
				20-50cm	Struc_20-50cm
				> 50cnm	Struc>50cm
				Shrubs 0.5-2m	Shrb_0.5-2m
				Shrubs > 2m	Shrb>2m
Cultivation	f	4	Plot level presence or absence of a suite of cultivation factors, from no cultivation to current standing crop	No Cultivation	NoCult
				Standing Crop	StdCrp
				Recent Cultivation (past 3 years)	RecCult
				Old Cultivation (4 or more years)	OldCult
Distance to the sea	c	1	A measure of the shortest distance per plot from the mean spring high water mark	Distance to the sea (m)	Dis2Sea

Table S3.2 List of species indicative of good and poor Machair quality, cultivated and fallowed Machair, taken from the Common Standards Monitoring Guidance for sand dune habitats, Joint Nature Conservation Committee (2004). Nomenclature follows Stace (2010).

Genus	Species	Poor-Quality	Good-Quality	Cultivated	Fallowed
Achillea	*millefolium*			x	x
Aira	*praecox*		x		
Anacamptis	*pyramidalis*		x		
Anagallis	*arvensis*			x	
Anchusa	*arvensis*			x	x
Arenaria	*serpyllifolia*			x	x
Atriplex	*patula*			x	x
Campanula	*rotundifolia*		x		
Carex	*arenaria*		x		
Cerastium	*diffusum*			x	x
Cerastium	*fontanum*		x		
Chrysanthemum	*segetum*			x	x
Cirsium	*acaule*	x			
Cirsium	*arvense*	x			
Cirsium	*dissectum*	x			
Cirsium	*eriophorum*	x			
Cirsium	*heterophyllum*	x			
Cirsium	*palustre*	x			
Cirsium	*tuberosum*	x			
Cirsium	*vulgare*	x			
Coeloglossum	*viride*		x		
Crepis	*capillaris*		x		
Dactylorhiza	*fuchsii*		x		
Dactylorhiza	*incarnata*		x		
Dactylorhiza	*lapponica*		x		
Dactylorhiza	*maculata*		x		
Dactylorhiza	*majalis*		x		
Dactylorhiza	*praetermissa*		x		
Dactylorhiza	*purpurella*		x		
Dactylorhiza	*traunsteineri*		x		
Erodium	*cicutarium*		x	x	x
Euphorbia	*helioscopia*			x	
Euphrasia	*anglica*				x
Euphrasia	*arctica*				x
Euphrasia	*cambrica*				x
Euphrasia	*campbelliae*				x
Euphrasia	*confusa*				x
Euphrasia	*foulaensis*				x
Euphrasia	*frigida*				x
Euphrasia	*heslop-harrisonii*				x
Euphrasia	*marshallii*				x
Euphrasia	*micrantha*				x
Euphrasia	*nemorosa*				x
Euphrasia	*officinalis*		x		x
Euphrasia	*ostenfeldii*				x
Euphrasia	*pseudokerneri*				x
Euphrasia	*rivularis*				x
Euphrasia	*rostkoviana*				x
Euphrasia	*rotundifolia*				x
Euphrasia	*salisburgensis*				x
Euphrasia	*scottica*				x
Euphrasia	*tetraquetra*				x
Euphrasia	*vigursii*				x
Fumaria	*bastardii*			x	x
Fumaria	*capreolata*			x	x
Fumaria	*densiflora*			x	x
Fumaria	*muralis*			x	x
Fumaria	*occidentalis*			x	x
Fumaria	*officinalis*			x	x

Table S3.2 Continued..

Genus	Species	Poor-Quality	Good-Quality	Cultivated	Fallowed
Fumaria	*parviflora*			x	x
Fumaria	*purpurea*			x	x
Fumaria	*reuteri*			x	x
Fumaria	*vaillantii*			x	x
Galium	*verum*		x		
Geranium	*molle*			x	x
Heracleum	*sphondylium*		x		
Lamium	*purpureum*			x	x
Linum	*catharticum*		x		
Listera	*cordata*		x		
Listera	*ovata*		x		
Lolium	*multiflorum*	x			
Lolium	*perenne*	x			
Lotus	*corniculatus*		x		
Myosotis	*arvensis*			x	x
Odontites	*vernus*		x		
Ophioglossum	*vulgatum*		x		
Papaver	*dubium*			x	
Papaver	*rhoeas*			x	x
Petasites	*albus*	x			
Petasites	*fragrans*	x			
Petasites	*hybridus*	x			
Phleum	*alpinum*	x			
Phleum	*arenarium*	x			
Phleum	*bertolonii*	x			
Phleum	*phleoides*	x			
Phleum	*pratense*	x			
Plantago	*lanceolata*		x		
Platanthera	*bifolia*		x		
Platanthera	*chlorantha*		x		
Polygala	*vulgaris*		x		
Polygonum	*aviculare*			x	x
Prunella	*vulgaris*		x		
Pseudorchis	*albida*		x		
Ranunculus	*acris*			x	x
Rhinanthus	*minor*		x		
Saxifraga	*tridactylis*			x	x
Sedum	*acre*		x		
Senecio	*aquaticus*	x			
Senecio	*cambrensis*	x			
Senecio	*cineraria*	x			
Senecio	*erucifolius*	x			
Senecio	*fluviatilis*	x			
Senecio	*jacobaea*	x			
Senecio	*paludosus*	x			
Senecio	*smithii*	x			
Senecio	*squalidus*	x			
Senecio	*sylvaticus*	x			
Senecio	*viscosus*	x			
Senecio	*vulgaris*	x			
Sinapis	*arvensis*			x	x
Thalictrum	*minus*		x		
Thymus	*polytrichus*		x		
Trifolium	*pratense*		x		x
Trifolium	*repens*		x		
Urtica	*dioica*	x			
Urtica	*urens*	x			
Veronica	*arvensis*				x
Viola	*canina*		x		
Viola	*riviniana*		x		
Viola	*tricolor*		x	x	x

S3.3 Use of field evidence to discriminate between different levels of grazing pressure and past cultivation.

S3.3.1 Identifying levels of grazing pressure

Grazing intensity at different levels could be assessed from vegetation height, presence of plant litter, and livestock dung. An abundance of dung, together with a uniformly short vegetation sward (with the exception of unpalatable plants) and little sign of litter, was taken as evidence of heavy grazing. Evidence of less intense ‘moderate’ grazing was a less uniform sward, with some dung and some litter. Light grazing was viewed where some evidence of dung, and vegetation could be seen, with larger mass of litter and much taller vegetation swards compared to moderate and heavy grazed areas.

S3.3.2 Identifying past cultivation use

Old, recent and current cultivation states were judged by assessing current vegetation and local land topography. Plots were marked as ‘current cultivation’ where standing crops were present; ‘recent cultivation’ where the vegetation compiled species typical of recent fallow and where plough burrows were still visible in the land; and ‘old cultivation’ where the plots had been cultivated in the past evidenced through old plough burrows but clearly was greater than 4 or more years ago evident from current plant species composition.

Chapter Four

Three decades of change in functional traits and functional diversity in a globally-rare semi-natural grassland: Investigating national and regional-scale shifts

ABSTRACT

Experimental studies have provided significant knowledge of how plant functional traits provide important linkages between the environmental control of vegetation and ecosystem function, particularly in relation to land use change.

This study takes this *a priori* knowledge of how functional traits respond to environmental change to help explain regional scale shifts in the vegetation composition of a globally-rare bio-type, identifying regions of conservation concern. Second, the utility of recently developed Functional Diversity (FD) indices in identifying the impacts of land use change on community assembly processes are demonstrated.

Community weighted mean traits values were significantly different for several traits, suggesting a significant national-scale change in the functional composition of the Machair grasslands between survey periods, while regional-scale analysis identified regions where considerably more change has occurred. Shifts occurred for both vegetative traits (vegetative height, specific leaf area, and leaf dry matter content) and regenerative traits (in particular pollination vectors). Through trait-environment linkages, regional shifts are identified to be a probable consequence of changing land use practices away from traditional low-intensity, rotational agriculture, towards either abandonment or agricultural intensification with important conservation implications.

Patterns of FD were assessed against expectation using comprehensive null-models. Results show habitat filtering to be linked to land use intensity and to be a significant process in shaping community vegetation of the Machair. Furthermore evidence of niche differentiation processes are found, empirically supporting the idea that community assembly processes are not mutually exclusive and at the scale studied are in operation primarily within different management units.

Understanding how functional traits respond to their environment provides an insight into how changing land use is impacting the biodiversity of this globally-rare biotype. From a methodological perspective, this study illustrates the benefits of using functional traits and FD indices in explaining community structure and determining drivers of temporal variation, and should allow for better conservation management in the long-term.

4.1 Introduction

Understanding the origins of variation within nature has long been central to conceptual developments in ecology. In plant ecology, the relative contributions of various deterministic and stochastic processes driving variation have underpinned the niche (Hutchinson 1957), neutral (Hubbell 2001) and limiting similarity (MacArthur and Levins 1967) theories, shaping current debates in species community assembly. However, the manner in which plant community variation is quantified is changing (Cadotte et al. 2011), as ecologists increasingly shift their focus away from a taxonomic-based to a trait-based perspective (Petchey and Gaston 2006). Driving this shift is a growing consensus that a trait-based view of community variation may far outweigh the utility of one solely centred on taxonomic diversity (TD) *per se* in explaining the structure and function of ecological communities (McGill et al. 2006).

In the realm of plant science, several studies have focused on the response of functionally-important species in terms of ecosystem functions and environmental change (e.g. Garnier et al. 2007; Flynn et al. 2009; Laliberté et al. 2010; Mayfield et al. 2010; Lavorel et al. 2011; Pakeman 2011b). This facet of functional diversity (FD), i.e. the variation in functional traits within ecological communities, focuses on 'functional response traits', i.e. traits that vary consistently in response to changes in environmental factors (Lavorel and Garnier 2002). Functional response trait diversity can be seen as an indicator of processes governing community assembly, as trait-environment linkages are governed by processes of functional trait filtering under varying environmental conditions (Keddy 1992) and at varying hierarchical spatial scales (Diaz et al. 1998). Moreover, they can show the impact of perturbations or identify ecological gradients, providing the ability to link shifts in management, climate and biogeochemistry to changes in vegetation characteristics (Pakeman et al. 2009).

This field of comparative trait ecology is a very active area of research and has prompted a surge in the development of new and improved metrics for quantifying FD. Over the last decade, single unit measures of functional group number have been progressively replaced by ones that decompose FD into complimentary indices, taking account of species abundance and avoiding trivial relations with TD (Mason et al. 2005; Cornwell et al. 2006; Villéger et al. 2008; Laliberté and Legendre 2010). Examination of these indices has shown the potential to increase the detail in which ecologists can explore hypotheses relating FD to community assembly rules and ecosystem function. For example, Mouchet et al. (2010) suggest separate components of functional diversity, i.e. richness, divergence and evenness as first proposed by Mason et al. (2005) to respond differently to different community assembly processes; demonstrating the potential for functional diversity components, that measure species and abundances in functional trait space, to distinguish between niche filtering, limiting similarity and to an extent neutral assembly processes. The application of these indices has also been shown by Pakeman (2011a) to explain how land use practices influence community assembly, identifying clear linkages between low functional richness and high functional evenness along disturbance gradients. From a conservation perspective, knowledge of how functional diversity is related to the environment is of utmost importance as "only if we know in some detail how plant functional types and particular species persist in the community can we then advise adequate procedures for vegetation management and conservation" (Grime 2006, p.256).

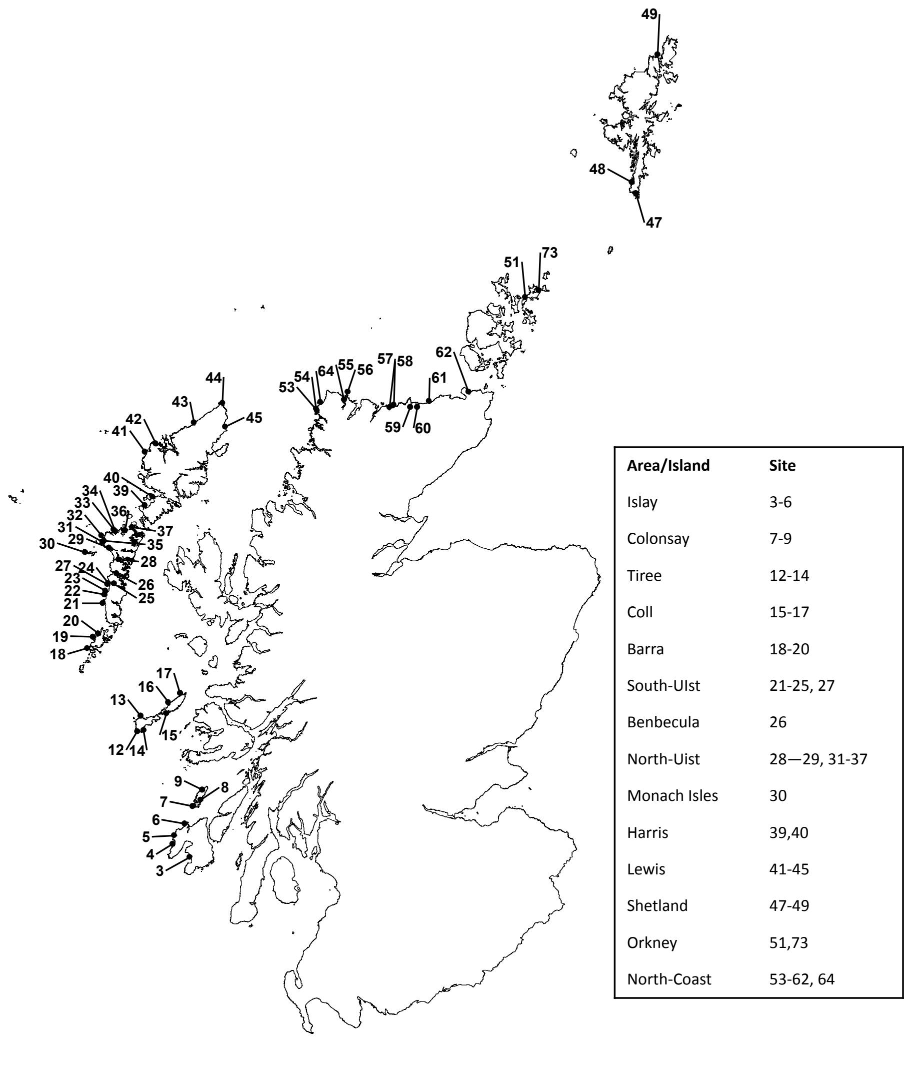
This work focuses on the functional trait composition of a globally-rare semi-natural grassland termed 'Machair'. These habitats are renowned for their biodiversity importance, listed on Annex I of the EC Habitats and Species Directive. The biodiversity value of the Machair grasslands is recognised at least in part to be attributable to the century-long associations with human land use (Angus and Dargie 2002). Site management techniques include those typical of traditional crofting practices i.e. small low-yielding crops (typically grain, often unfenced strips and minimal use of synthetic fertiliser or herbicides), fallow areas (usually 2-year duration), hay meadow and winter-grazed rough grassland. The scale of operation has more in common with pre-World War I agriculture than the largely intensified agriculture typical of most farming areas in the United Kingdom and Europe today. However, the biodiversity that includes the cultural heritage of these habitats is threatened. Socio-economic changes alongside a declining and ageing population (Mackenzie 2007), have resulted in some shifting away from these traditional agricultural practices towards a more modern or less time-consuming approach. Consequently cropped areas have become larger (often fenced), plough depths have increased through use of larger and heavier machinery and synthetic fertilisers progressively augment organic alternatives. However, the intensity of these changes is not consistent across all regional areas of Machair grassland, as recently shown by Pakeman et al. (2011a).

Through use of a national-scale spatio-temporal dataset first collated in 1975-1977 and then again in 2009-2010, this study has two main aims: first, to utilise current knowledge of how functional traits respond to environmental change (particularly land use change) to infer drivers of vegetation change among Machair grasslands, and second, to investigate the impacts of land use change on community assembly processes through the application of several recently developed FD indices. Specifically, this study addresses the following four questions: (i) do functional trait signatures vary between surveys? (ii) Can changes in trait signatures identify changes in land use intensity? (iii) Are changes in traits correlated to changes in FD? And: (iv) do changes in FD between surveys help explain how land use impacts on community assembly processes?

4.2 Materials and Methods

4.2.1 Data collection

Baseline data were taken from the Scottish Coastal Survey (1975-1977; Shaw et al. 1983), from which a sub-sample of sites (n=56), known to include Machair communities were selected for re-survey (Fig. 4.1). Vegetation was re-surveyed in 1548 plots between June and September in 2009 and 2010; the relative abundance of all higher plant species in 5 m × 5 m quadrats was recorded. Number of plots per site ranged from 9 to 61 (Appendix 4.1). To minimise sources of error between surveys, sites were re-surveyed as close to the original survey date as possible. Relocation accuracy was estimated to be within ± 10m of the original geographical British National Grid co-ordinates. The exact location of the plot was selected using information on the original vegetation composition. Where there was uncertainty of the original plot location, it was omitted. This method for revisitation surveys of non-permanent vegetation samples has been shown to be effective in detecting temporal change with confidence (Ross et al. 2010).



Area/Island	Site
Islay	3-6
Colonsay	7-9
Tiree	12-14
Coll	15-17
Barra	18-20
South-UIst	21-25, 27
Benbecula	26
North-Uist	28—29, 31-37
Monach Isles	30
Harris	39,40
Lewis	41-45
Shetland	47-49
Orkney	51,73
North-Coast	53-62, 64

Fig. 4.1 Distribution of study sites across Scotland. For site information see Appendix 4.1.

4.2.1.1 Plant Functional Traits

Traits were selected for analysis based on their known or assumed utility as functional response-traits. In particular response traits correlated to disturbance regimes were chosen. Nine traits, 3 vegetative and 6 reproductive were assembled from two main sources (Table 4.1), BiolFlor (Klotz et al. 2002) and LEDA (Kleyer et al. 2008), with seed longevity taken from Thompson et al. (1997). Missing data were supplemented with data from floras and by averaging data from congeners. Remaining gaps contributed ~ 2 % of the total.

Table 4.1 Selected response traits used in the analysis and in the calculation of functional diversity of Scottish Machair grasslands. Source information, coding details and response to environmental gradients are detailed.

Trait	Abbreviation	Details	Attributes	Ecosystem Response Gradient
log(Vegetation height) (m)	VH	Vegetative, continuous		Disturbance (Westoby 1998) Grazing intensity (Westoby 1998)
log(Seed mass) (mg)[1]	SM	Reproductive, continuous		Dispersal (Pakeman 2008) Disturbance (Pakeman 2008)
Leaf dry matter content* (mg/g)[2]	LDMC	Vegetative, continuous		Disturbance gradient (Pakeman 2011a) Productivity (Garnier et al. 2004)
log(Seed longevity)[3]	SL	Reproductive, continuous		Disturbance (Pakeman 2004)
Specific leaf area* (mm^2/mg)[2]	SLA	Vegetative, continuous		Litter-decomposition (Mokany et al. 2008) Productivity (Garnier et al. 2004)
Terminal velocity (m/s)[2]	TV	Reproductive, continuous		Dispersal (Green and Johnson 1989) Disturbance (Green and Johnson 1989)
Flowering start (month)[1]	Flst	Reproductive, 1-12		Land use change (Garnier et al 2007) Grazing intensity (Pakeman 2004; Garnier et al 2007) Disturbance (Pakeman 2004; Garnier et al 2007)
Pollen vector[1] i. Insects ii. log(self)+1 iii. Wind	PV i. Insects ii. Self iii. Wind	Reproductive, 0,1	not insect pollinated, insect pollinated, not self pollinated, self pollinated, not wind pollinated, wind pollinated	Grazing intensity (Pakeman 2011a) Disturbance (Pakeman 2011a)
Vegetative spread[1] i. Stoloniferous ii. log(Rhizomatous)+1	VS i. Stol ii. Rhz	Reproductive, 0,1	not stoloniferous, stoloniferous, not rhizomatous, rhizomatous	Colonization ability (Pakeman 2004) Grazing intensity (Pakeman 2004)

Leaf economics discriminates between two of the main functional strategies, exploitative and conservative species (Albert et al. 2010). *Sources:* [1]BiolFlor; [2]LEDA; [3]Thompson et al. (1997).

4.2.2 Data Analysis

All plots from the original survey were allocated a National Vegetation Classification (NVC; Rodwell 1991a, 1991b, 1992, 2000) using the software package 'TABLEFIT' (Hill 1993). The original and re-survey datasets were sub-divided to include only those plots that were allocated a NVC representative of Machair grassland, as defined by Angus (2006). This sub-set data matrix comprised 348 species from 853 plots, 56 sites and 14 regions, encompassing almost the entire Machair resource of Scotland. The 14 regions represented relatively independent geographical units.

4.2.2.1 Community Weighted Mean Traits

In explaining how biota influence key ecosystem processes, it has been argued that abundant species are often more functionally important simply because of greater representation (*see Mass Ratio Hypothesis*, Grime 1998). To account for this proposed insensitivity of ecosystem function to the functional properties of subordinate species, community weighted mean values (hereafter CWM) were calculated for each trait as the mean of trait values in the community, weighted by the relative abundance of the species (Diaz et al. 2007). Significant change among CWM traits was tested by paired t-tests, whilst regional differences were investigated using restricted maximum likelihood (REML) methods in the 'lme' function of R. In these REML analyses, a general linear model to the variance across two nested spatial scales were fitted i.e. plot (quadrat) within landowner as the random effect. The model was applied to all CWM traits, using log transformation when required. To investigate correlative trends between traits, principal component analysis was used, analysing CWM trait matrix, standardized to mean 0 and unit variance.

4.2.2.2 Functional Diversity Indices

Functional diversity was measured following the recommendations of Mason et al. (2005) through three individual metrics of FD, Richness (FRic), Evenness (FEve) and Divergence (FDiv) of Villéger et al. (2008), and a fourth, 'Functional Dispersion' (FDis) of Laliberté and Legendre (2010). These indices explore different facets of FD in multi-dimensional trait space, and have been shown to correlate with different processes of community assembly (Mouchet et al. 2010).

FRic represents the minimum convex hull volume of functional space occupied by the community (Cornwell et al. 2006), FEve represents the regularity of distribution in abundance within this volume and FDiv represents the divergence in the distribution of the species traits. Functional Dispersion was included in the analysis to represent the spread of the species within the volume of functional trait space. Although FRic can estimate Functional Dispersion, it is, however, positively influenced by species number (Villéger et al. 2008). In contrast, FDis (see Laliberté and Legendre 2010) is little influenced by species number; therefore ensuring the measure of FDis was not trivially related to species richness (Laliberté et al. 2010). Descriptions of how Fric, Feve, FDiv and FDis are calculated are displayed in Figures S4.1 and S4.2, taken from Villéger et al. (2008) and Laliberté and Legendre (2010).

4.2.2.3 Null models

To test if the FD indices measured were significantly different from expected, each value of FRic, FEve, FDiv and FDis for each plot were compared against those from 999 simulated assemblages. These simulated assemblages were constructed using all species recorded within a site and across both surveys. For each site, the randomisation procedure retained the species identity (selecting species only from the site's species pool) but randomly exchanging the species abundances (species not recorded at a site, had, therefore, an abundance of zero). Throughout the selection process, each species had an equal probability of being selected. This method of simulated assemblage construction maintains site species richness and more importantly, the pattern of within-site abundance, i.e. a matrix swap randomisation (Manly 1995). An expected value was calculated at each level of species richness as the mean of the values given by the 999 randomisations. From these simulations, a Z-score was calculated for each of the FD measures at plot (i.e. quadrat) scale (eqn1):

$$Z = \left(\frac{Obs - Exp^{x}}{Exp^{SD}} \right) \qquad \text{(eqn1)}$$

This expresses the deviation of observed vs expected FD, where *Obs* is the FD obtained from the observed data, while Exp^{x} and Exp^{SD} is the mean and standard deviation of the randomisations for the relevant species richness level. Each functional diversity measure was subject to single sample student's t-test to investigate significant deviations in Z-scores from expected. Differences in mean functional diversity Z-score measures between different study areas were assessed using REML (model structure mirrored that of CWM analysis).

Finally, to correlate any identified shifts in functional diversity indices with shifts in response traits (i.e. change in CWM), the change in Z values over time were subject to linear-mixed regression against the temporal change in principal component Axes 1 and 2 (see *Community Weighted Mean Traits*). The random term included landowner nested within area. Differences in co-variation between the random terms were also assessed. Quadratic relationships were tested but only reported if they were a significant improvement over the linear regression, i.e. if they displayed a lower Akaike Information Criterion (AIC; Burnham and Anderson 2002).

All analyses were carried out in R version 2.11.0 (R Development Core Team 2011), with the calculation of all functional diversity indices, and community weighted means performed using the 'FD' package of Laliberté and Legendre (2010). Principal component analysis was implemented using the R package 'vegan' (Oksanen et al. 2011). Restricted maximum likelihood (REML) methods were implemented in the R package 'nlme' (Pinheiro et al. 2011).

4.3 Results

4.3.1 Shifts in Community Weighted Mean Traits

Eight out of twelve traits changed significantly over the 33-year time period (Table 4.2). Refinement of the CWM analysis focused at the finer regional-scale revealed significant shifts across all traits, with each region exhibiting significant change in at least one trait. A number of patterns were observed: In all cases, an increase in Vegetative Height (VH) was coupled by a significant decline in Specific Leaf Area (SLA; Table 4.3). Principal component analysis revealed VH and SLA to display a strong opposing positive and negative relationship with Axis 1 respectively (Fig. 4.2). Regions could be separated into two distinct groups; those showing no significant change in vegetative traits (Benbecula, Coll, Colonsay and Shetland) from those with significant change in all vegetative traits between the two survey periods (Barra, Monachs, N.Uist and S.Uist).

Among the regenerative traits tested, only one region (N.Uist) revealed a significant change in all traits. Benbecula, Lewis and Monachs showed little change in regenerative traits, with trait shifts reported only for pollen vector or vegetative spread. As might be expected, seed mass was positively correlated with terminal velocity, and further positively correlated with rhizomatous spread, vegetation height and self-pollinating species. Insect-pollinated species revealed significant shifts for 7 out of 14 regions surveyed. Moreover, all shifts, with one exception (Sanday) displayed an overriding decline in this trait attribute, found also to be positively correlated with Axis 2 (Fig. 4.2). The opposite was true for wind-pollinated species (Table 4.3), which correlated closely with leaf dry matter content, flowering start, and partially with stoloniferous species (Fig. 4.2). In summary, there was a clear separation between several traits across Axes 1 and 2. The total inertia explained (Axis 1 ≈ 39%, Axis 2 ≈ 20%), indicating that the first two axes explain a substantial amount of the variation.

Table 4.2 Summary of Scottish national-scale shifts in Community Weighted Mean (CWM) response traits in Machair grassland assemblages, assessed through multiple paired t-tests. ^, $p < 0.06$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Displayed values are the CWMs (back-transformed for VH and SM).

	x1976	x2010	t	Sig
Vegetation height	0.40	0.42	4.00	***
Seed mass	1.32	1.47	2.84	***
Leaf dry matter content	241.39	246.87	5.16	***
Specific leaf area	20.44	20.17	-1.92	^
Flowering start	5.57	5.67	6.36	***
Terminal velocity	2.64	2.67	2.52	*
Seed longevity	0.38	0.38	-1.00	n.s
Wind pollinated	0.69	0.73	4.75	***
Insects pollinated	0.42	0.39	-4.38	***
Self pollinated	0.34	0.34	-0.04	n.s
Rhizomatous spread	0.27	0.27	0.44	n.s
Stoloniferous spread	0.60	0.62	2.16	*

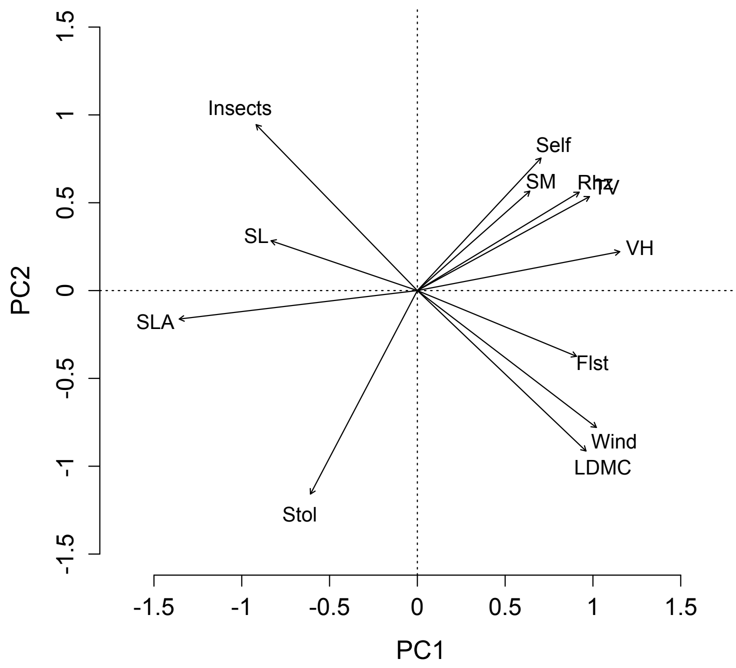


Fig. 4.2 Plot of the principal component analysis of cover weighted mean response traits derived form two surveys of Scottish Machair grassland, standardised to mean 0 and unit variance. Abbreviations are as follows: VH: Vegetation Height, SM: Seed Mass, LDMC: Leaf Dry Matter Content, SLA: Specific Leaf Area, Flst: Flowering start, TV: Terminal Velocity, SL: Seed Longevity, Wind, Insects and Self: Pollination mechanisms, Rhz: Rhizomatous spread, Stol: Stoloniferous Spread.

4.3.2 Difference of Functional Diversity Indices from Expectation

Functional Richness (FRic) and Functional Dispersion (FDis) were found in almost all cases to be lower than expected (Table 4.4); exceptions were N.Uist and the Monachs (2010 only). For FRic, only 4 in 1976 (Colonsay, Monach, S.Uist and Tiree), and 2 in 2010 (Colonsay and N.Uist) of the 14 regions surveyed did not display significant departures from expectation. For FDis, non-significant departures from expectation were found within regions Benbecula, Colonsay and the Monachs, although the FDis for Colonsay in 1976 was close to significant ($p = 0.051$).

The patterns were quite different for FDiv. Here values lower than expected were noted only for Colonsay, Harris and the Shetlands Isles for the 1976 survey, while all other regions showed FDiv to be significantly higher than expected. For the 2010 data, only the Shetland isles displayed values lower than expected. Results suggest overall, greater FDiv occurred throughout the surveyed regions than would be expected by chance (Table 4.4).

It is clear from the results that for the 14 regions surveyed, Functional Evenness had a tendency to be close to expectation. The only exceptions were found in 2010, where Barra and the Shetland Isles displayed significantly lower evenness values. General patterns of higher or lower than expected FD values were less obvious for Functional Evenness, a likely artefact of maintaining values close to expectations (Table 4.4).

Table 4.3 Summary of significant temporal shifts for Community Weighted Mean response traits for the 14 Scottish Machair grassland regions surveyed. ^, $p < 0.06$; ,**'** $p < 0.05$; **''**, $p < 0.01$; **'''**, $p < 0.001$. Displayed values are the mean differences (back-transformed for VH and SM). Values in bold indicate significant temporal shifts between surveys.

	VH	SM	LDMC	SL	SLA	TV	Flst	Insects	Self	Wind	Stol	Rhz
Barra	**0.05''**	0.01	**23.1'''**	**-0.04'''**	**-1.9'''**	**0.21'''**	**0.33'''**	**-0.11''**	-0.04	**0.18'''**	**0.14'''**	-0.05
Benbecula	0.05	0.38	9.02	0.01	-1.87	<0.01	-0.08	**-0.17'**	0.12	**0.16''**	-0.09	0.08
Coll	0.02	-0.11	3.58	<0.01	0.85	-0.01	**0.11'**	-0.04	-0.03	<0.01	0.02	0.01
Colonsay	-0.04	-0.36	0.73	**0.05'**	1.97	**-0.22'**	-0.12	<0.01	-0.03	-0.03	**-0.19'**	**0.2''**
Harris	0.05	**0.38'**	11.6	-0.03	**-2.31''**	**0.21''**	-0.03	-0.1	0.02	0.05	-0.03	0.09
Islay	0.02	-0.29	**11.4'**	0.02	1.1	-0.08	**0.17'**	**-0.09'**	**-0.09'**	**0.09''**	0.05	0.02
Lewis	<0.01	-0.14	5.62	<0.01	0.78	<0.01	0.09	<0.01	-0.01	-0.03	**0.08''**	**-0.06'**
Monachs	**0.08'''**	0.32	**12.4'**	-0.02	**-2.47'''**	0.11	0.03	**-0.13''**	0.04	**0.1''**	0.03	0.05
North-Coast	-0.02	-0.05	-1.72	<0.01	**1.24''**	-0.03	**-0.09'**	0.03	0.03	-0.03	0.02	-0.04
North-Uist	**0.03''**	**0.37'''**	**8.13'''**	**-0.01'**	**-1.91'''**	**0.13'''**	**0.22'''**	**-0.08'''**	<0.01	**0.08'''**	<0.01	**0.04'**
Sanday	-0.02	-0.03	**-12.9''**	**0.03'**	**1.33'**	-0.04	-0.07	**0.08'**	-0.01	**-0.07'**	<0.01	-0.05
Shetland	-0.01	-0.25	8.9	<0.01	0.95	**-0.18''**	0.03	**-0.09'**	-0.03	0.06	**0.1'**	-0.07
South-Uist	**0.05'''**	**0.70'''**	**6.31'**	<0.01	**-0.92'**	0.05	**0.21'''**	-0.02	<0.01	**0.05''**	<0.01	<0.01
Tiree	-0.01	0.11	-1.96	0.02'	**1.35''**	-0.07	-0.03	0.02	0.02	**-0.05'**	-0.01	0.01

Table 4.4 Results of single sample t-tests and REML analysis of the four FD Z-values for the 14 Scottish Machair grassland regions surveyed. Significant departures of FD values from expectations for the two surveys are represented by: ^, $p < 0.06$; **'** $p < 0.05$; **''**, $p < 0.01$; **'''**, $p < 0.001$. Displayed values are the mean differences. d.f. = degrees of freedom, + or – values indicate the gains (+) or falls (-) for the retrospective indices. Significant shifts, assessed using REML methods are represented by: ^, $p < 0.06$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

		FRic_Z				**FDiv_Z**				**FEve_Z**				**FDis_Z**			
	d.f.	*x*1976	*x*2010	+/-	sig	*x*1976	*x*2010	+/-	sig	*x*1976	*x*2010	+/-	sig	*x*1976	*x*2010	+/-	sig
Barra	46	-0.46'''	-0.45'''	+		0.25'	0.08	-		-0.01	-0.54'''	-	**	-0.31''	-0.81'''	-	***
Benbecula	13	-0.80'''	-0.54'	+		0.48'	0.44'	-		0.09	-0.15	-		-0.38	-0.13	+	
Coll	67	-0.16'	-0.45'''	-	**	0.40'''	0.59'''	+		-0.16	-0.05	+		-0.31'''	-0.52'''	-	^
Colonsay	9	-0.12	-0.43	-		-0.07	0.90'''	+	**	0.02	-0.15	-		-0.46^	-0.21	+	
Harris	22	-0.89'''	-1.03'''	-		-0.20	0.02	+		-0.18	-0.07	+		-0.90'''	-0.67''	+	
Islay	37	-0.59'''	-0.89'''	-	*	0.34''	0.19	-		-0.02	-0.11	-		-0.41'''	-0.80'''	-	**
Lewis	79	-0.34'''	-0.71'''	-	***	0.44'''	0.27'''	-		0.07	0.10	+		-0.54'''	-0.88'''	-	***
Monachs	34	-0.16	0.50''	+	***	0.64'''	0.68'''	+		0.37	-0.11	-	*	-0.17	-0.05	+	
North Coast	91	-0.62'''	-0.68'''	-		0.58'''	0.51'''	-		-0.05	0.00	+		-0.22'	-0.42'''	-	*
North Uist	187	0.12'	0.02	-		0.32'''	0.30'''	-		0.09	-0.05	-		-0.34'''	-0.36'''	-	
Sanday	47	-0.32''	-0.45'''	-		0.50'''	0.24''	-	^	0.06	0.08	+		-0.86'''	-0.84'''	+	
Shetland	33	-0.47'''	-0.53'''	-		-0.05	-0.25	-		-0.10	-0.48'''	-		-0.32'	-0.30'	+	
South Uist	97	-0.08	-0.36'''	-	***	0.61'''	0.52'''	-		0.04	-0.01	-		-0.16''	-0.38'''	-	*
Tiree	83	-0.09	-0.63'''	-	***	0.25''	0.43'''	+		-0.20'	0.01	+		-0.70'''	-1.03'''	-	***

4.3.3 Shifts In Functional Diversity Indices

Functional Richness declined in 11 of the 14 areas, of which 5 were significant (Coll, Islay, Lewis, S.Uist and Tiree). Of the 3 areas where FRic increased, change was only significant among Monach Isles ($p < 0.001$, Table 4). Patterns of change among areas for FDiv, FEve and FDis were less uniform, with increases and decreases separating the different areas. Relatively few of the changes reported for Functional Divergence (Colonsay^{+ve}) and Evenness (Barra^{-ve} and Monach^{-ve}) were significant. Despite opposing patterns of change in FDis, all significant shifts (6 of 14) were reported as a decline. A decline in Dispersion for Coll was marginally significant ($p = 0.053$).

Regressions of the between-survey differences of PC Axis 1 and Axis 2 scores with the mean change in FD Z-scores are presented in Fig. 4.3. For Axis 1, Functional Richness, Divergence and Dispersion displayed significant, positive linear relationships, whereas evenness failed to display any correlation with Axis 1 (Table 4.5; Figures 4.3a-d). Functional Richness and again Functional Evenness were un-correlated with Axis 2. Functional Divergence revealed a significant negative relationship with Axis 2. Conversely, Functional Dispersion displayed a strong positive and highly significant relationship with Axis 2 (Table 4.5, Fig. 4.3h). Investigation of random effect variance revealed much of the variation explained to be at the finer spatial scale (i.e. land-owner; Table 4.5).

Table 4.5 Results of linear mixed regression analysis assessing the correlations between the temporal shifts in principal component (PC) Axis 1 and Axis 2 against Scottish national-scale temporal shifts in the four measures of functional diversity in Machair grassland. FRic = Functional Richness; FEve = Functional Evenness; FDiv = Functional Divergence; FDis = Functional Dispersion. PC axes are taken from a PC analysis of the community weighted mean traits (Fig. 4.2).

			variance explained		
PC1~	intercept	coef	regional	land-owner	p value
FRic	0.18	0.44	0.02	0.05	<0.001
FDiv	0.06	0.98	0.02	0.07	<0.001
FEve	0.09	0.19	0.02	<0.001	0.22
FDis	0.19	0.61	0.00	0.07	<0.001
PC2~	intercept	coef	regional	land-owner	p value
FRic	0.16	-0.02	0.03	0.05	0.84
FDiv	0.06	-0.47	0.02	0.07	<0.001
FEve	0.07	0.07	0.01	<0.001	0.60
FDis	0.12	0.94	0.01	0.06	<0.001

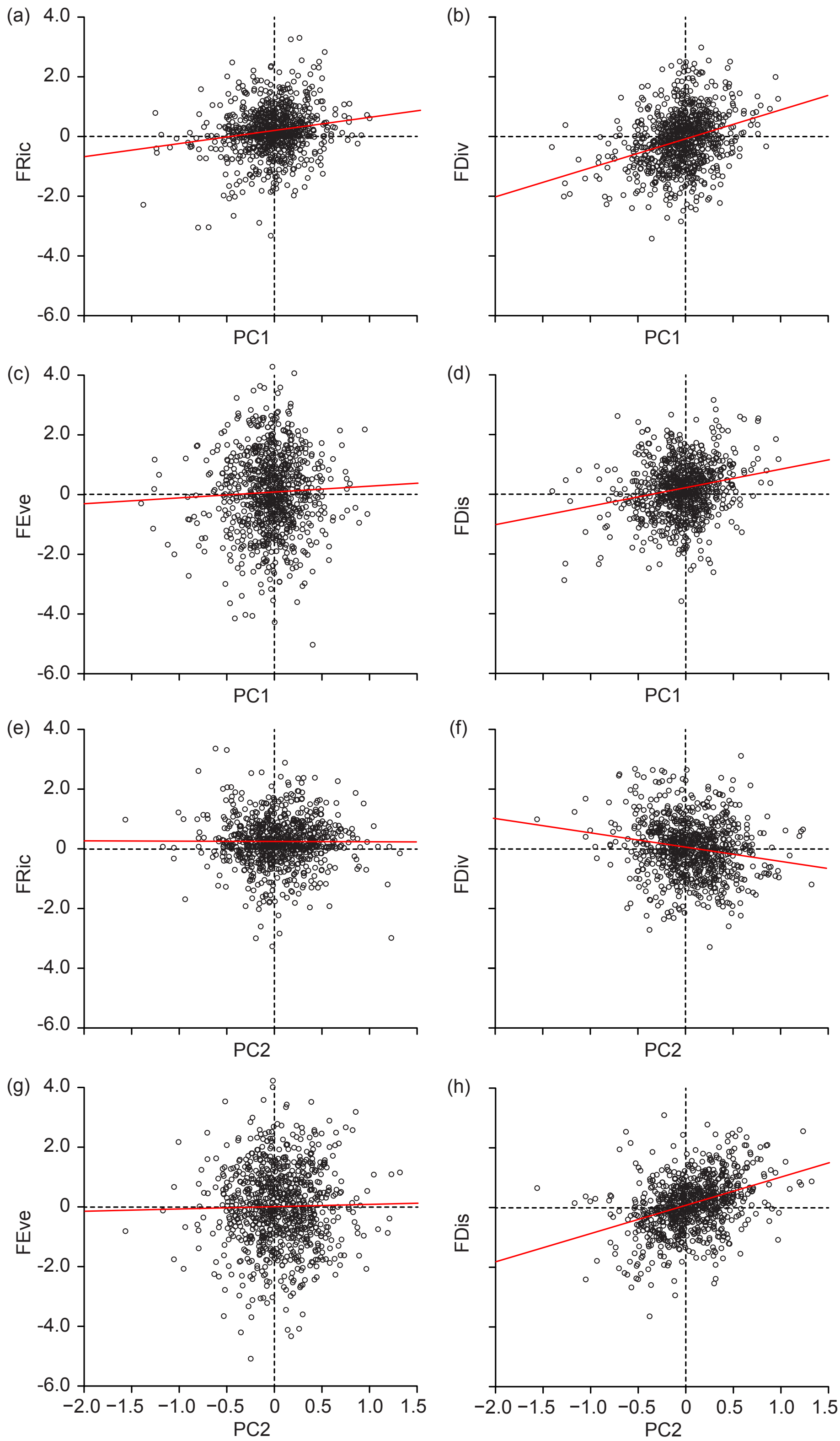


Fig. 4.3 Plot of correlation analyses assessing relationships between temporal shifts in PC Axis 1 (a-d) and PC Axis 2 (e-h) of community weighted mean traits (derived from two surveys of Scottish Machair grassland) between national-scale shifts in the four functional diversity indices. FRic = Functional Richness; FEve = Functional Evenness; FDiv = Functional Divergence; FDis = Functional Dispersion.

4.4 Discussion

4.4.1 Shifts in Community Weighted Mean Traits

Two-thirds of the trait attributes tested (8/12) showed significant shifts between survey years (Table 4.2), suggesting a general change in functional trait composition between the years 1976 and 2010. What is clear from the REML analysis on community weighted mean (CWM) traits is that certain regions (e.g. N.Uist and Barra) have seen considerably more change in functional traits than others (e.g. Coll), suggesting certain regions have witnessed greater change in land use than others.

Multivariate analysis of the community weighted means of traits revealed correlative patterns between many of the response traits (Fig. 4.2). Among the vegetative traits, opposing patterns between vegetation height (VH) and specific leaf area (SLA) were found where gains in VH were met by declines in SLA, similar to those expected along a disturbance gradient (Westoby 1998). Identification of significant differences between compositions of these vegetative traits permits inferences regarding the intensity of land use between the Machair grassland regions. For example, in a grassland environment, where grazing intensity is high, plant species would be expected to be shorter and invest fewer resources per unit leaf area (as plants become selected for quick regrowth after defoliation), as was found for the N.Coast, Sanday and Tiree. In contrast the opposing pattern would be expected for communities subject to less intense grazing management, as was found for Barra, Monachs, N.Uist, S.Uist and arguably Harris. Results here typically reflect the views of landowners for some of these regions, the consensus being towards a general decline in sheep and cattle grazing for North and South Uists and relatively no change for Sanday and Tiree (Pakeman et al. 2011a).

With the exception of Harris, regions subject to significant declines in SLA were also subject to significant increases in leaf dry matter content (LDMC). Recent work has shown declines in LDMC to be linked with increasing productivity and disturbance gradients (Pakeman et al. 2011b). This fits well with responses of VH and SLA found here, providing further support that the regions Barra, Monachs, N.Uist and S.Uist are less intensively managed today than they were in 1976. However, caution is required when making inferences from single trait analyses involving LDMC as the complete picture may be obscured, due to potential quadratic response of LDMC to disturbance (e.g. Pakeman and Marriott 2010).

Of the regenerative traits, the metric for wind pollination and similarly insect pollination produced the greatest change between surveys (8/14 and 7/14 regions) displaying overall gains in wind pollination, compared with overall declines in insect pollinated plants. Wind pollination is prevalent in many grass and sedge species. A greater abundance of grasses over forbs can be brought about through several different scenarios, including both increased and reduced disturbance. For example, increased grazing pressure may result in the grazing-out of forb species; however this goes against the view of a general decline in livestock for many Machair regions (Pakeman et al. 2011a). In contrast, reduced grazing intensity should permit longer lived grasses to predominate. Whichever process is the driver of change, it appears to reduce significantly the prevalence of insect-pollinated plants. The general decline in the latter between surveys has significant conservation implications, particularly for bumblebee (*Bombus*) populations, where the north-westerly fringes of Scotland are considered important strongholds for *Bombus distinguendus* and *Bombus muscorum*, two of the UK's rarest species (Goulson et al. 2005). Forage plants, on which these species depend, are associated strongly with the flower-rich Machair habitats that formed as a result of the traditional, low-intensity, rotational-agriculture (Angus 2001). However, socio-economic change has resulted in some shifting away from traditional management practices (Pakeman et al. 2011a), consequently impacting upon the vegetation composition (Chapter 3). It is possible that the increased use of inorganic fertiliser (Pakeman et al. 2011a) evident also in the findings of Chapter 3, may account for the decline in insect-pollinated species. Application of inorganic fertiliser may have two effects: (1) reduce the need to leave land fallow, thus reducing weed species and other species that ultimately depend on them, and (2) reduce the application of seaweed, de-stabilising the soil, and increasing tall grass species tolerant of sand burial (e.g. *Ammophila arenaria* and *Leymus arenarius*). The only region to indicate an increase in insect-pollinated species was Sanday. This is in agreement with significant increases in the cover of species typical of Machair grassland and Machair fallows for this region (Chapter 3).

4.4.2 Differences of Functional Diversity Indices from Expectation

Values of FRic, with few exceptions, were consistently lower than expected. This suggests the functional trait space for most community assemblages surveyed were more constrained (i.e. more similar) than would be expected by chance (Cornwell et al. 2006). This suggests a general prevalence of habitat filtering across these areas, whereby environmental conditions act as filters, reducing the spectrum of functional trait strategies among co-existing species (Zobel 1997). These environmental filters probably display a spatial hierarchy, where climate constrains the functional diversity at the broadest-scale, as shown for taxonomic diversity (Chapter 2), and land use constrains the functional diversity at much more local scales. This pattern of lower than expected FRic values were consistent with findings of Cornwell et al. (2006) and Pakeman (2011a). Measures of Functional Evenness mostly showed no difference from a random pattern. Barra and Shetland were two exceptions, where among the re-survey data only, values were significantly lower than expectation. Theoretical expectation from Mouchet et al. (2010) suggests that lower than expected values of FEve, also indicates habitat filtering.

Unsurprisingly, patterns of FDis mirrored those of FRic, as the Functional Dispersion of any given species assemblage is limited by its functional trait space. Further, FRic is a binomial metric of Functional Dispersion, as the volume of the minimum convex hull that encapsulates all species; thus it is a multivariate analogue of the range, albeit sensitive to sub-ordinate species (Laliberté and Legendre 2010). This similarity in behaviour or FRic and FDis was reflected in the correlation analysis (Table S4.1). As expected, FDis revealed a moderate, positive correlation with FRic. This is in agreement with the findings of Laliberté and Legendre (2010), who replicated 20,000 artificial species communities in which to run comparisons of FDis with other FD indices. However, results also revealed FDis Z-values to be significantly correlated to species richness, albeit weakly (Table S4.1).

Patterns in FDiv showed opposing trends to FRic and FDis. Deviations from expectations were found to be positive, (Table 4.4), providing empirical support of functional trait divergence, indicating species coexistence through niche differentiation (MacArthur and Levins 1967). This process of community assembly is typically governed through competitive exclusion (Grime 1973). However, empirical support for such a mechanism of species co-existence remain sparse, as the interactions are complex and sensitive to environmental disturbance. Consequently, disturbance (e.g. land use change) has the potential to alter greatly the role that these processes play in community assembly (Mayfield et al. 2010) and mask the patterns of niche differentiation at certain spatial scales (Stubbs and Wilson 2004).

4.4.3 Shifts in Functional Diversity Indices

Functional Richness indicates the degree of habitat filtering in operation (Cornwell et al. 2006; Mouchet et al. 2010). As well as evidence for filtering effects (see *Difference of Functional Diversity Indices from Expectation*), examination of FRic Z-scores between surveys clearly shows an increase in number and or intensity of these filters on the species community in the re-survey (Table 4.4). Regression analysis of CWM ordination axes revealed such filter effects to be highly correlated with SLA and VH (Fig. 4.2), as a strong positive correlation was revealed between FRic with Axis PC1 (which accounts for the majority of variation in the data, Fig. 4.3a; Table 4.5). Given that gains in SLA and VH can be linked to decreasing land use intensity (see, *Shifts in Community Weighted Mean Traits*), results suggest that the degree of habitat filtering increases as the intensity of land use increases, supporting the findings of Flynn et al. (2009), Laliberté et al. (2010) and Pakeman (2011a). Coll, Islay, Lewis, S.Uist and Tiree, all showed significant declines in FRic, suggestive of increased land use intensity since the original survey. Significant departures from this pattern were only found for the Monach Isles. Here, not only did FRic increase significantly between surveys ($p < 0.001$), FRic values for the re-survey were also shown to be significantly greater than expectation ($p < 0.001$, Table 4.4). The Monachs have had no permanent residents and no cultivation since 1949 (Perring and Randall 1971); results here are thus indicative of the impacts of near abandonment of agriculture on these remote islands.

Functional Dispersion is a measure of spread between species within the functional trait space. FDis increases when species are functionally 'dissimilar', and decreases when species are functionally 'similar' (Laliberté and Legendre 2010). In this study significant shifts in FDis were all negative (Table 4.4), indicating compositional shifts towards functionally-similar species for 6 regions (Barra, Islay, Lewis, N.Coast, S.Uist and Tiree), this indicates greater environmental filtering as niche space is reduced in size. It is possible for this to result from increased land use disturbance, as further analyses showed FDis to be positively correlated with PC Axis 1 (Fig. 4.3d), representative of a disturbance gradient through increased VH and decreased SLA at high values of Axis 1 (Fig. 4.2). Results suggest reduced disturbance promotes functional dissimilarity, resulting in greater functional trait space, supporting the findings of Pakeman (2011a).

Shifts in FDis can have potential conservation implications and has been discussed in terms of functional redundancy (i.e. the number of species contributing similarly to an ecosystem function; Laliberté et al. 2010), and its importance for ensuring high ecosystem resilience. By definition: ecosystem resilience is the ability to return to its former state following perturbation (Diaz and Cabido 2001). According to Laliberté et al. (2010), reduced FDis indicates a loss of resilience as species become functionally more similar in the way they respond to environmental disturbances. This raises concerns over the ability of Machair grasslands for some regions to adapt to environmental change without loss of function or diversity. However, although resilience is strongly influenced by the traits of the dominant plant species (Lepš et al. 1982; MacGillivray et al. 1995), it arguably is also equally governed by the presence of rare species (Walker et al. 1999). Here analyses were based on weighted abundance measures, downplaying the importance of rare species in favour of more predominate species (Grime 1998), suggesting caution is required here when making inferences regarding redundancy and resilience. Nevertheless it does provide a benchmark for further investigation.

Significant shifts in values of FDiv and FEve between surveys were less prevalent. Functional Divergence: a measure of how abundance is distributed within the volume of functional trait space (Villéger et al. 2008) was found to change for Colonsay, increasing significantly ($p < 0.001$). Of the CWM traits for Colonsay, metrics of vegetative spread showed the greatest significant change (see, *Shifts in Community Weighted Mean Traits*). Previous studies have shown that trait attributes concerned with vegetative spread are associated with change in grazing intensity. Pakeman (2004) showed rhizomatous species increased with reduced grazing intensity while stoloniferous species increased with increased grazing intensity. In this study, these trait attributes were shown to be positively (rhizomatous spread) and negatively (stoloniferous spread) correlated with PC Axes 1 and 2, respectively (Fig. 4.2), as was also FDiv (Fig. 4.3; Table 4.5). Therefore, the patterns suggest FDiv declines along a gradient of grazing intensity, further indicating that processes of niche differentiation may be more prevalent among vegetation communities subject to less intense disturbances.

Finally FEve, a measure of how functional space is occupied within a community, declined significantly for Barra and the Monachs, indicating species to be less regularly-spaced in trait space in the re-survey (Villéger et al. 2008). Recent findings of Pakeman (2011a), revealed FEve to be promoted with increased levels of disturbance, suggesting Barra and Monachs to be less disturbed today than in the 1970s. This is representative once again of near abandonment of the Monachs. It also raises concerns of a decline in management on the Isle of Barra.

4.4.4 Community assembly processes

Several mechanisms have been proposed to explain community assembly in ecological systems (McArthur and Levins 1967; Hubbel 2001, Grime 1973), and recently, there is increasing evidence that these processes are not mutually exclusive (Fukami et al. 2005; Kraft et al. 2008). For example, research on community assembly in a coastal biotype in California (Cornwell and Ackerly 2009) found that both habitat filtering and competitive exclusion co-occurred, simultaneously shaping the community assembly of local plant species. Patterns of FDiv and FRic reported here are certainly in agreement with the latter, suggesting that processes of niche differentiation (i.e. trait divergence) to occur within a framework of habitat filtering (i.e. trait convergence), with neither process showing prevalence over the other at the spatial scale surveyed.

However, while these mechanisms are fundamental to community assembly, their respective influence on the trait divergence-convergence balance are unlikely to be consistent across different spatial scales (Freschet et al. 2011). For this national-scale study, much of the variation explained was shown to reside among the finer spatial-scaling factor ‘land-owner’ (Table 4.5). Thus, the equal prevalence of convergence and divergence reported here, is likely to be linked to environmental processes (abiotic or biotic) influenced at the land management scale, and to a lesser extent to environmental processes at the regional scale. This highlights the need for future conservation decisions of the Machair grassland to be addressed at a site-specific level.

4.5 Conclusions

This study shows there have been considerable shifts in the functional composition at national- and regional-scales for the Machair grassland communities of Scotland; an internationally rare biotope. For many of the traits selected for study, there is much *a priori* evidence linking certain traits to environmental conditions and ecosystem function (Pakeman 2004; Garnier et al. 2007; Pakeman et al. 2011b). Reported here, through correlation analysis, it is apparent that there are clear linkages between shifts in species functional trait composition with changes in land use and management since 1976. Through utilising these trait-environment linkages, several regions of potential conservation concern have been identified. Barra and N.Uist are subject to significantly less management today than in 1976, while N.Coast and Tiree may be managed too intensively. Multiple trait analysis revealed Sanday to display an increase in land use intensity, yet this was the only region to display an increase in insect-pollinated species, suggesting management here is more in-line with conservation targets for Machair grassland, but does bring attention to a worrying decline in insect pollinator species shown across all other Machair regions.

Furthermore, through applied use of functional diversity indices, evidence of trait convergence (habitat filtering) and trait divergence (niche differentiation) revealed the simultaneous operation of community assembly processes at the regional scales that were surveyed. For several regions, significant declines in community resilience and increased environmental constraints were apparent. Understanding the drivers of these patterns is paramount for advising adequate conservation management procedures for the on-going protection of Machair grasslands. Here, this study demonstrates the combined utility of functional traits and FD indices, as easily measurable and highly informative metrics, to aid ecologists in explaining the structure and function of ecological communities.

REFERENCES

Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. and Lavorel, S. 2010. A multi-trait approach reveals the structure and the relative importance of intra-vs. Interspecific variability in plant traits. Functional Ecology 24, 1192-1201.

Angus, S. 2001. The Outer Hebrides: moor and machair. The White Horse Press, Cambridge/Isle of Harris, UK.

Angus, S. and Dargie, T. 2002. The UK Machair habitat action plan: progress and problems. Botanical Journal of Scotland 54, 63-74.

Angus, S. 2006. De tha Machair? Towards a Machair definition. Sand dune Machair 4, 7-22. Aberdeen Institute for Coastal Science and Management, Aberdeen.

Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference. Springer, New York.

Cadotte, M.W., Carscadden, K. and Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48, 1079-1087.

Cornwell, W.K., Schwilk, D.W. and Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87, 1465-1471.

Cornwell, W.K. and Ackerly, D.D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monograpghs 79, 109-126.

Diaz, S., Marcelo, C. and Fernando, C. 1998. Plant functional traits and environmental filers at a regional scale. Journal of Vegetation Science 9, 113-122.

Diaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16, 627-655.

Diaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. and Robson, M. 2007. Incorporating plant functional diversity effects in ecosystem service assessment. Proceedings of the National Academy of Sciences 104, 20684-20689.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinaria, N., Richers, B.T. et al. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12, 22-33.

Freschet, G.T., Dias, A.T.C, Ackerly, D.D., Aerts, R., van Bodegom, P.M. et al. 2011. Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. Global Ecology and Biogeography 20, 755-765.

Fukami, T., Bezemer, T.M., Mortimer, S.R. and van der Putten, W.H. 2005. Species divergence and trait convergence in experimental plant community assembly. Ecology Letters 8, 1283-1290.

Garnier, E., Cortez, J., Bille´ s, G., Navas, M.-L., Roumet, C. et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630-2637.

Garnier, E., Lavorel, S. Ansquer, P., Castro, H., Cruz, P. et al. 2007. A standardized methodology to assess the effects of land use change on plant traits, communities and ecosystem functioning in grasslands. Annals of Botany 99, 967–985.

Goulson, D., Hanley, M.E., Darvil, B., Ellis, J.E. and Knight, M.E. 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1-8.

Greene, D.F. and Johnson, E.A. 1989. A model of wind dispersal of winged or plumed seeds. Ecology 70, 339-347.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344-347.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems immediate, filter and founder effects. Journal of Ecology 86, 902-910.

Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. Journal of Vegetation Science 17, 255-260.

Hill, M.O. 1993.. TABLEFIT, Version 1.0 for Identification of vegetation types. Institute of Terrestrial Ecology, Huntingdon.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hutchinson G. 1957. Concluding remarks. Cold Spring Harbor Synposium on Quantative Biology. 22, 415-427.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3, 157-164.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K. et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96, 1266-1274.

Klotz, S., Kühn, I. and Durka, W. 2002. BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Bundesamt für Naturschutz, Bonn – Bad Godesberg.

Kraft, N.J.B., Valencia, R. and Ackerly, D.D. 2008. Functional traits and niche-based tree community assembly in an Amazonian Forest. Science 322, 580-582.

Laliberté, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P. et al. 2010. Land use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters 13, 76-86.

Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545-556.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D. et al. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. Journal of Ecology 99, 135-147.

Lepš, J., Kosinová, J.O. and Rejmánek, M. 1982. Community stability, complexity and species life-history strategies. Vegetatio 50, 53–63

MacArthur, R.H. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101, 377-385.

MacGillivray, C.W., Grime, J.P and ISP Team. 1995. Testing predictions of the resistance and resilience of vegetation subjected to extreme events. Functional Ecology 9, 640–649

Mackenzie, A.F.D. 2007. The contribution of crofting in the 21st Century. Committee of Inquiry on Crofting. < www.croftingenquiry.org> accessed 19.01.2012..

Manly, B.J.F. 1995. A note on the analysis of species co-occurrences. Ecology 76, 1109-1115.

Mason, N.W.H., Mouillot, D., Lee, W.G. and Wilson, B.J. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. OIKOS 111, 112-118.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. and Vesk, P.A. 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for response of species and functional trait diversity to land use change. Global Ecology and Biogeography 19, 423-431.

McGill, B,J., Enquist, B.J., Weiher, E. and Westoby M. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21, 178-185.

Mokan, K., Ash, J. and Roxburgh, S. 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. Journal of Ecology 96, 884-893.

Mouchet, M.A., Villéger, S., Mason, N.W.H. and Mouillot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24, 867-876.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B. et al. 2011. vegan: Community Ecology Package. R package version 1.17-8. http://CRAN.R-project.org/package=vegan

Pakeman, R.J. 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. Journal of Ecology 92, 893-905.

Pakeman, R.J., Reid, C.L., Lennon, J.J. and Kent, M. 2008. Possible interactions between environmental factors in determining species optima. Journal of Vegetation Science 19, 201-208.

Pakeman, R.J., Lepš, J., Klyer, M., Lavorel, S. and Garnier, E. 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. Journal of Vegetation Science 21, 148-159.

Pakeman, R.J. and Marriott, C.A. 2010. A functional assessment of the response of grassland vegetation to reduced grazing and abandonment. Journal of Vegetation Science 21, 683-694.

Pakeman, R.J. 2011a. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. Journal of Ecology 99, 1143-1151.

Pakeman, R.J. 2011b. Multivariate identification of plant functional response and effect traits in an agricultural landscape. Ecology 92, 1353-1365.

Pakeman, R.J., Huband, S., Kriel, A. and Lewis, R.J. 2011a. Changes in the management of Scottish Machair communities and associated habitats from the 1970s to the present. Scottish Geographical Journal 127, 267-287.

Pakeman, R.J., Lennon, J.J. and Brooker, R.W. 2011b. Trait assembly in plant assemblages and its modulation by productivity and disturbance. Oecologia 167, 209-218.

Perring, F.H. and Randall, R.E. 1971. An annotated flora of the Monach Isles national nature reserve, Outer Hebrides. Botanical Journal of Scotland 41, 431-444.

Petchey, O.L. and Gaston, K.J. 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9, 741-758.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and the R Development Core Team. 2011. nlme: Linear and nonlinear mixed effects models. R package version 3.1-102.

R Development Core Team 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rodwell, J.S. 1991a. British plant communities. Volume 1: Woodlands and scrub. University Press Cambridge.

Rodwell, J.S. 1991b. British plant communities. Volume 2: Mires and heaths. University Press Cambridge.

Rodwell, J.S. 1992. British plant communities. Volume 3: Grasslands and montane communities. University Press Cambridge.

Rodwell, J.S. 2000. British plant communities. Volume 5: Maritime communities and vegetation of open habitats. University Press Cambridge.

Ross, L.C., Woodin, S.J., Hester, A., Thompson, D.B.A. and Birks, H.J.B. 2010. How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? Plant Ecology and Diversity 3, 1-8.

Shaw, M.W., Hewett, D.G. and Pizzey, J.M. 1983. Scottish coastal survey. Institute of Terrestrial Ecology. Bangor Research Station, Bangor, Gwynedd.

Stubbs, W.J. and Wilson, J.B. 2004. Evidence for limiting similarity in a sand dune community. Journal of Ecology 92, 557-567.

Thompson, K., Bakker, J.P. and Bekker, R.M. 1997. The soil seed banks of north west Europe: methodology, density and longevity. Cambridge University Press, Cambridge.

Villéger, S., Mason, N.W.H. and Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290-2301.

Walker, B.H., Kinzig, A. and Langdrige, J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2, 95–113.

Westoby, M. 1998. A-leaf-height-seed LHS. plant ecology strategy scheme. Plant and Soil 199, 213-227.

Zobel, M. 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? Trends in Ecology and Evolution 12, 266-269.

Appendix 4.0

Appendix 4.1 Site Information and climate data for each of the sites used in the analysis.

ID	Site Location	Site Name	Plots	East	North	Annual Mean Temp (^{0}C)		Precipitation (mm yr^{-1})		Growing Degree Units		Potential Evapo-transpiration (mm d^{-1})		Aridity		Monthly Mean Humidity (%)	
						1961-77	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*
3	Islay	Laggan	34	130	654	9.0	9.4	1195	1355	1250.3	1416.1	63.7	62.3	0.66	0.66	84.0	83.2
4	Islay	Machir Bay	29	121	663	8.3	8.8	1141	1376	1079.2	1203.1	56.7	55.8	0.65	0.62	84.3	83.5
5	Islay	Saligo bay	25	121	666	8.9	9.4	1102	1321	1232.0	1374.4	59.1	58.3	0.67	0.64	84.1	83.2
6	Islay	Gruinart	53	130	673	9.0	9.5	1181	1401	1275.9	1438.8	61.9	61.0	0.66	0.64	83.2	82.2
7	Colonsay	Oronsay	33	135	688	9.0	9.7	1128	1206	1374.1	1513.6	61.5	59.8	0.66	0.66	83.5	82.2
8	Colonsay	Garvard	19	135	691	9.0	9.7	1128	1208	1363.4	1503.9	61.5	59.8	0.66	0.66	83.5	82.3
9	Colonsay	Kiloran	18	140	697	9.2	9.8	1171	1240	1385.8	1536.7	62.3	60.7	0.65	0.66	83.6	82.2
12	Tiree	West Tiree	54	094	743	9.0	9.6	1056	1232	1279.9	1407.1	55.0	55.1	0.64	0.64	85.2	82.9
13	Tiree	North Tiree	27	096	747	9.0	9.5	1089	1259	1267.8	1399.4	55.6	55.7	0.64	0.63	85.1	82.8
14	Tiree	Crossapoll	22	099	743	8.9	9.5	1063	1232	1257.8	1388.8	55.6	55.6	0.64	0.63	85.1	82.8
15	Coll	West Coll	61	113	753	9.0	9.5	1099	1272	1285.2	1409.7	55.8	55.9	0.64	0.64	84.8	82.4
16	Coll	Clabhach	26	117	756	8.8	9.4	1175	1432	1250.2	1379.0	55.9	55.6	0.63	0.61	84.8	82.5
17	Coll	Gallawach	32	121	761	8.9	9.5	1302	1579	1296.5	1417.1	56.4	56.0	0.59	0.59	84.6	82.3
18	Barra	Vatersay	20	063	795	8.9	9.6	1270	1241	1336.7	1446.3	52.1	52.1	0.63	0.63	86.3	84.1
19	Barra	West Barra	9	064	801	8.7	9.4	1412	1332	1283.0	1388.4	50.3	50.3	0.60	0.61	86.4	84.1
20	Barra	N Barra	27	069	806	8.9	9.6	1535	1388	1335.2	1446.6	52.2	52.3	0.58	0.61	86.5	84.1
21	South Uist	Daliburgh	48	073	822	8.8	9.4	1363	1364	1220.7	1363.9	54.7	54.3	0.61	0.63	86.5	83.9
22	South Uist	Ormiclate	31	073	830	8.8	9.4	1337	1404	1213.6	1354.4	54.0	53.8	0.60	0.62	86.4	83.7
23	South Uist	Howbeg	16	074	835	8.7	9.3	1305	1398	1178.2	1334.8	54.3	53.8	0.61	0.62	86.7	83.9
24	South Uist	N.Stiligarry	23	075	840	8.6	9.3	1278	1308	1178.9	1328.6	53.9	53.8	0.61	0.64	86.8	83.9
25	South Uist	Loch Bee	46	075	844	8.6	9.3	1256	1307	1179.7	1329.5	53.9	53.8	0.62	0.64	86.7	83.8
26	Benbecula	Borve	20	077	850	8.6	9.3	1168	1280	1178.7	1334.2	54.4	54.3	0.64	0.64	86.2	83.2
27	South Uist	S.Stilligarry	29	075	837	8.6	9.2	1297	1409	1160.4	1321.5	54.6	54.0	0.61	0.62	86.7	83.9
28	North Uist	Baleshare	50	078	860	8.6	9.2	1118	1254	1181.2	1356.4	57.2	56.5	0.66	0.66	85.9	82.8
29	North Uist	Kirkibost	13	075	864	8.5	9.2	1098	1257	1164.7	1349.2	58.0	56.9	0.66	0.65	86.1	83.0
30	Monach	Monach Isles	37	063	862												
31	North Uist	Paible	11	072	867	8.6	9.2	1080	1274	1169.9	1317.5	53.8	53.3	0.65	0.63	86.2	83.2
32	North Uist	Hosta	22	071	873	8.6	9.2	1079	1306	1163.5	1299.2	52.6	52.1	0.64	0.62	86.3	83.3
33	North Uist	Vallay	27	077	876	8.5	9.1	1132	1349	1153.9	1312.0	55.8	54.8	0.64	0.62	86.4	83.4
34	North Uist	Leathann	30	081	876	8.6	9.2	1091	1328	1182.5	1329.9	55.7	54.9	0.65	0.63	86.5	83.5
35	North Uist	Balranald	23	070	869	8.6	9.2	1080	1286	1168.6	1311.9	53.5	53.1	0.64	0.62	86.3	83.2
36	North Uist	Robach	26	087	876	8.6	9.2	1083	1326	1193.8	1328.3	55.4	54.9	0.65	0.62	86.4	83.4
37	North Uist	Berneray	57	090	882	8.6	9.2	1083	1393	1201.2	1281.7	51.3	51.8	0.63	0.60	86.7	83.7
39	Harris	Northton	31	098	891	6.9	7.5	1219	1678	819.9	830.9	43.1	44.1	0.55	0.52	87.0	83.9
40	Harris	Luskintyre	27	106	898	8.5	9.2	1619	1890	1199.4	1316.9	58.7	57.8	0.55	0.55	86.7	83.7

Appendix 4.1 Continued..

ID	Site Location	Site Name	Plots	East	North	Annual Mean Temp (^0C)		Precipitation (mm yr^{-1})		Growing Degree Units		Potential Evapo-transpiration (mm d^{-1})		Aridity		Monthly Mean Humidity (%)	
						1961-77	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*	*1961-77*	*1990-06*
41	Lewis	Uig	24	103	932	8.2	9.0	1329	1635	1169.2	1274.5	52.7	51.6	0.62	0.60	87.0	83.7
42	Lewis	Valtos	19	109	936	8.4	9.2	1432	1659	1236.5	1338.2	54.4	53.5	0.60	0.60	86.9	83.5
43	Lewis	Barvas	27	135	951	7.9	8.5	1192	1415	1038.6	1189.4	56.8	54.6	0.64	0.63	87.0	83.6
44	Lewis	Tolsta	25	154	948	7.4	8.1	1175	1419	917.3	1062.9	54.7	52.2	0.64	0.62	87.4	83.9
45	Lewis	Tolsta	25	154	948	7.4	8.1	1175	1419	917.3	1062.9	54.7	52.2	0.64	0.62	87.4	83.9
47	Shetland	Quendale	30	438	111	7.8	8.4	995	1027	927.1	1070.8	46.4	45.8	0.68	0.69	84.9	82.3
48	Shetland	Scousburgh	25	437	111	7.7	8.3	1063	1087	899.6	1046.6	46.1	45.3	0.67	0.68	85.3	82.7
49	Shetland	Breckon	25	453	120	7.1	7.8	1135	1107	851.2	993.9	50.7	50.3	0.66	0.68	86.2	83.0
51	Orkney	Holland	27	363	103	7.7	8.3	938	994	919.6	1049.1	47.6	48.3	0.67	0.69	86.4	84.8
53	North Coast	Oldshore More	27	220	958	7.9	8.5	1136	1386	1036.6	1224.2	59.1	59.2	0.66	0.67	85.6	83.4
54	North Coast	Sheigra	24	218	960	8.1	8.7	1071	1357	1057.7	1214.1	53.1	53.8	0.64	0.64	86.0	83.9
55	North Coast	Durness	23	237	967	7.7	8.4	1281	1481	947.7	1174.3	57.9	57.5	0.63	0.63	85.6	83.6
56	North Coast	Faraid Head	24	239	970	7.8	8.5	1320	1531	980.7	1197.2	56.8	56.4	0.61	0.61	85.7	83.6
57	North Coast	Bettyhill	27	269	961	7.9	8.5	926	1037	1080.1	1223.1	60.2	60.8	0.70	0.71	85.2	83.2
58	North Coast	Farr Bay	24	271	962	7.6	8.2	856	993	1025.1	1156.8	59.9	60.3	0.72	0.72	85.2	83.1
59	North Coast	Strathy	20	283	965	7.8	8.3	868	957	969.8	1085.0	56.7	57.2	0.70	0.70	85.4	83.4
60	North Coast	Melvich	18	288	964	7.3	7.8	961	1060	919.2	1055.9	60.7	60.8	0.70	0.69	84.6	82.7
61	North Coast	Reay	22	296	965	8.1	8.7	899	932	1077.2	1248.7	61.8	62.3	0.71	0.73	84.7	83.0
62	North Coast	Dunnet	23	322	969	7.5	8.1	840	995	939.4	1091.7	62.2	62.3	0.73	0.71	84.6	83.4
64	North Coast	Sandwood	20	221	964	7.4	8.1	1146	1426	910.5	1087.8	55.5	55.5	0.64	0.63	85.8	83.7
73	Orkney	Overbister	28	370	104	7.9	8.5	933	964	959.3	1094.6	48.4	49.0	0.67	0.71	86.4	84.7

N.B. No climate data available for the Monach Isles.

Supplementary Material (S4)

Table S4.1 Pearson's correlation matrix between species richness and functional diversity (FD Indices: FRic = Functional Richness; FEve = Functional Evenness; FDiv = Functional Divergence; FDis = Functional Dispersion. Z = deviation of observed vs expected FD . ^, p < 0.06; ', *Ip* < 0.05; '', p < 0.01; ''', p < 0.001. Data derived from two surveys of Scottish Machair grassland.

	Simpson	Sp.count	FRic	FDiv	FEve	FRic_Z	FDiv_Z	FEve_Z
Sp.count	0.40'''							
FRic	0.12'''	0.22'''						
FDiv	-0.24'''	0.06'	-0.23'''					
FEve	-0.18'''	-0.22'''	-0.09'''	0.12'''				
FDis	0.13'''	0.02	0.51'''	-0.41'''	-0.03			
FRic_Z	-0.14'''	-0.16'''						
FDiv_Z	-0.11'''	0.08''				0.05'		
FEve_Z	-0.05'	-0.07''				0.01	0.10'''	
FDis_Z	-0.23'''	-0.17'''				0.31'''	0.32'''	0.05'

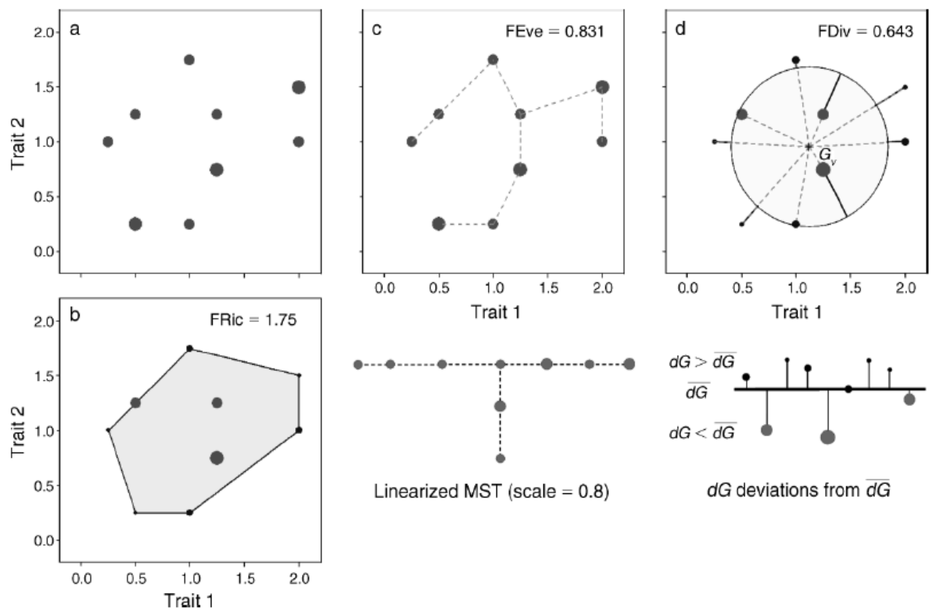


Fig. S4.1 Estimation of the three functional diversity indices in multidimensional functional space. For simplification, only two traits and nine species are considered. (a) The points are plotted in the space according to the trait values of the corresponding species. Circle diameters are proportional to species abundances. In (b), the convex hull is drawn with a solid black line; the points corresponding to the vertices are black, and the convex hull volume is shaded in gray. The functional richness (FRic) corresponds to this volume. (c) The minimum spanning tree (MST, dashed line) links the points. Functional evenness (FEve) measures the regularity of points along this tree and the regularity in their abundances. For convenience, the tree is plotted stretched under the panel. (d) The position of the centre of gravity of the vertices (''G_V,'' black cross), the distances between it and the points representing the species (gray dashed lines), and the mean distance to the centre of gravity (large circle with the black line border). The deviation of the distances from the mean corresponds to the length of the black line linking each point and the large circle with the black line border. This distribution is also represented under the panel. The more the high abundances are greater than the mean, the higher the functional divergence (FDiv). (Figures and text from Villéger et al. 2008).

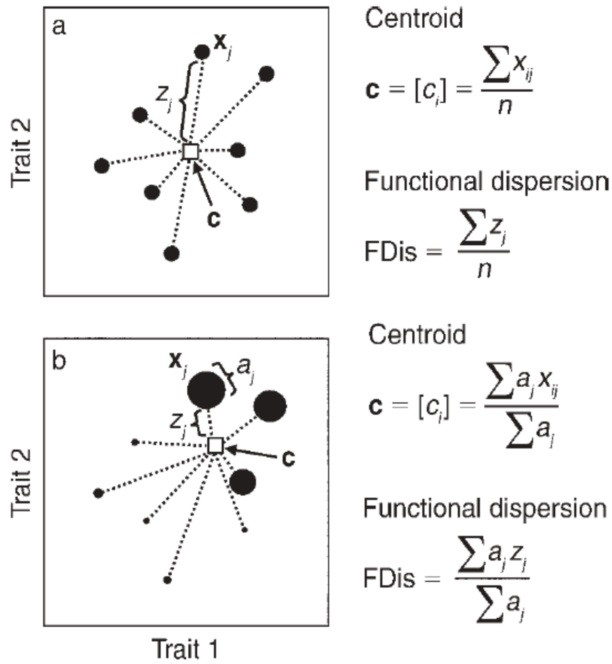


Fig. S4.2 An example showing how functional dispersion (FDis) is computed. The n individual species in a two-dimensional trait space are represented by black circles whose sizes are proportional to their abundances. Vector xj represents the position of species j, c is the centroid of the n species (white square), zj is the distance of species j to centroid c, and aj is the abundance of species j. In panel (a), all species have equal abundances (i.e., presence–absence data). In that case, c 1⁄4 [ci], where ci is the mean value of trait i, and FDis is the mean of distances z of individual species to c. In panel (b), species have different abundances. In that case, the position of c is weighted by the species relative abundances, such that it shifts toward the more abundant species. Individual distances z of species to c are weighted by their relative abundances to compute FDis. (Figures and text from Laliberté and Legendre 2010).

Chapter Five

Climate and spatial turnover captures temporal beta diversity patterns in semi-natural grasslands

ABSTRACT

This research investigated how temporal turnover of a globally-rare grassland (Machair) has responded to different measurable components of climate. It focused on three variables: (i) mean minimum temperature, (ii) water balance and, (iii) growing degree days. From 5km monthly data, mean, variance, long-term trends, between-year similarity and relative climatic extremes were calculated and the response of temporal turnover predicted. Models were also run including and excluding spatial turnover to gauge its contribution to temporal turnover. Several measures of β-diversity were used, each representing a different measurable component of turnover, (1) species richness difference component (β_{gl}), (2) species replacement components (β_{sim}), (3) 1 & 2 combined (β_{sor}) and (4) species relative abundance dissimilarity (β_{BC}). Patterns of climate and spatial turnover were assessed in terms of their response and ability to capture temporal variation in Machair vegetation between the different indices. The index inclusive of relative abundance information (β_{BC}) was expected to out perform the presence/absence indices.

Results suggest climate to have a small, yet significant, influence on temporal turnover patterns of Machair grasslands. The response of turnover to different measurable components of climate was found to vary depending on the turnover index used, that is, it depended on the component of turnover examined. Only long-term trends in water balance displayed a consistent pattern across all indices (a positive association). Both temporal change in climate and the extent of turnover were found to vary in space. Patterns were found to correlate with regions of Scotland's coast where biodiversity has declined, and other regions where biodiversity has increased over time. Spatial turnover was shown to significantly enhance model capability in capturing temporal variation across three of the four indices of turnover. Contrary to expectations, the relative abundance index was out-performed by the Sørensen index (β_{sor}).

5.1 Introduction

One way of quantifying patterns in biodiversity is to measure β-diversity (Whittaker 1960, 1972). Generally defined as the variation in the identities of species among sites (Legendre 2008), β-diversity provides a conceptual link between biodiversity at local scales (α diversity) and regional scales (γ diversity; Whittaker 1960, 1972). Indeed the study of β-diversity lies at the origins (though not under this name) of modern biogeography; the study of which species live where and why (Darwin 1859; Wallace 1870). Nonetheless, compared to its α- and γ- counterparts, studies of β-diversity have received surprisingly little attention until recently. In parallel to the increasing recognition of β-diversity as a key concept for understanding ecosystem function (Legendre et al. 2005), the number of studies directly addressing β-diversity has greatly increased over the last decade (Anderson et al. 2011).

However, unlike α– and γ-diversity, β-diversity is not singularly defined; even Whittaker (1960) used the term 'β-diversity' in its most general sense, encompassing many different phenomena. This has resulted both in many measures of β-diversity in the ecological literature (Koleff et al. 2003; Tuomisto 2010a,b) and a variety of statistical methods (Anderson et al. 2006; Tuomisto and Ruokolainen 2006; Legendre 2008; Baselga 2010; Podani and Schmera 2011) for analysing patterns in β-diversity.

Koleff et al. (2003) were the first to review comprehensively, various binary (presence/absence) measures of β-diversity, unifying multiple metrics as either (i) 'broad sense', i.e. measures that incorporate differences in species composition attributable to species richness components and or both richness and replacement components, and, (ii) 'narrow sense', i.e. measures that ignore the richness components altogether, focusing solely on the replacement component. Species replacement and species richness differences are two distinct components of species dissimilarity (Lennon et al. 2001; Baselga 2010), attributable to (i) a substitution of one species with another (replacement) and (ii), an imbalance in recruitment and extinction processes i.e. species losses and/or gains (richness differences).

These broad and narrow sense measures are almost always based on similarity/dissimilarity indices calculated from presence/absence information. However, β-diversity dissimilarity measures can also incorporate relative abundance information (Legendre and Legendre 1998), which is an important aspect of community structure (Anderson et al. 2011). Moreover, comparative analysis between presence/absence and relative abundance measures can provide useful insights into the nature of community level change (Anderson et al. 2006).

Koleff et al. (2003) and more recently Juranski et al. (2009) and Tuomisto (2010a,b) have provided extensive reviews of existing measures of β-diversity, including their mathematical interrelationships. These syntheses emphasize the complexity of β-diversity found in natural communities (the reasoning for the existence of so many measures) and provide a considerable advancement in knowledge of how different metrics perform.

The present study takes the multi-model approach of Anderson et al. (2011) to show that using different measures, which reflect different aspects of β-diversity, is potentially very useful. Furthermore, the methodological approach is extended beyond simple quantification of β-diversity by examining the relative importance of climatic factors for species compositional turnover in time. The ideas used to develop β-diversity as a measure of biodiversity across a landscape (spatial turnover) can be similarly applied to measure biodiversity within the same area through time (temporal turnover). It is then possible to evaluate processes structuring temporal biodiversity patterns, by relating patterns in temporal turnover to environmental gradients. The relative importance of environmental factors influencing species turnover, notably ecological sorting over environmental gradients is well studied (Tuomisto et al. 2003; Qian et al. 2005; Stegen et al. 2012). However most of these studies investigate spatial turnover, while temporal turnover has remained relatively less well studied. This is so, despite evidence that partitioning β-diversity into space and time can yield important insights into how biodiversity is maintained. Moreover, only a handful of studies have reported the influence of environmental drivers on the fundamentally different components that contribute to β-diversity using a multi-metric approach (Svenning et al. 2011; Carvalho et al. 2012). However, even these studies were restricted to spatial turnover.

Using a large spatio-temporal dataset of coastal grassland vegetation and climatic data of north-western Scotland, this study investigates the extent to which environmental sorting through climatic variation governs the different processes of temporal turnover. The methods of Lennon et al. (in prep.) are followed, breaking climatic variation down into separate measurable components: means, variances, long-term-trends, between-year similarity (autocorrelations) and climatic anomalies. This study aims to determine how different measurable components of climate influence temporal turnover of plant assemblages, particularly the richness and replacement components of turnover, using a suite of broad to narrow indices and a relative abundance index of turnover.

Given that temporal turnover measures compositional differences within sites at different times, one obvious driver is likely to be climate and its temporal variability. It is well reported that climate can operate as an environmental filter, governing the presence and abundance of species with traits for a particular climatic envelope (Keddy 1992; Díaz et al. 1998). Variation in climate should then, continuously permit or prevent species presence, or increase and decrease the abundance of species at the limit of their environmental space (Huntley et al. 2007). Similarly, smaller levels of environmental variation, or increased autocorrelation should have a stabilising effect on plant communities, reducing the rate at which species come and go from a community and also the rate at which species alter their abundance within assemblages.

Compositional change may also be linked to the rate and magnitude of climatic change. For example, theory suggests that the greater the rate of change, the greater the magnitude of (i) species compositional change, (ii) species distributional change and (iii) extinction (Huntley et al. 2010). Therefore with increasing magnitude of long-term climatic trends, increased species temporal turnover can be expected.

Finally, long-term impacts of episodic events have also been reported to promote species spatial and temporal turnover. Best studied for arid ecosystems in relation to the El Niño effect (i.e. irregular climatic oscillations whereby high rainfall is followed by extreme drought), time spent in relatively unusual climate regimes for a given area can have strong ecological consequences on plant species assemblages and ecosystem function (Polis et al. 1997; Holmgren et al. 2001).

This study therefore tests a series of hypotheses, previously derived by Lennon et al. (in prep.) for the effects of climatic means, variances, long-term trends, autocorrelation and relative climatic extremes on species temporal turnover. These were:

- (H1) Means: change in means will impact on species temporal turnover, but direction is unknown
- (H2) Variances: greater variance results in more species temporal turnover
- (H3) Long-term trends: steeper gradients of long-term change result in more species temporal turnover
- (H4) Similarity (autocorrelation): greater between year similarity results in less species temporal turnover
- (H5) Relative extremes (fat tail measure): greater time spent in relatively unusual climate regimes results in more species temporal turnover

In addition to these formal hypotheses, the relationship between temporal turnover and spatial turnover is investigated. It has been argued that temporal turnover in combination with spatial turnover are two aspects of a more general unified pattern known as the species-time-area-relationship (Alder et al. 2005; White et al. 2006). Theory suggests that if species are placed randomly throughout the landscape, increased temporal turnover will promote an increase in spatial turnover (Steiner and Leibold 2004). This positive association between spatial and temporal turnover has been reported in previous studies (Ptacnik et al. 2008; Ptacnik et al. 2010); however studies that directly evaluate this relationship when partitioned into richness and replacement components of β-diversity have not yet been attempted.

These ideas are tested, and results reported, of how climatic factors and spatial turnover influence temporal turnover within a globally-rare grassland ecosystem. Moreover, using a multi-metric approach it is asked if climate equally determines richness and replacement components of turnover, and investigate any inconsistencies between patterns that may be revealed. In addition, an abundance measure of β-diversity (Bray-Curtis) is used; extending information on species simple presence/absence to species composition, with the expectation that models using this abundance metric will better capture temporal variation compared with those with presence/absence metrics (H6).

5.2 Methods

5.2.1 Study site

The vegetation of the Scottish Machair grasslands and its associated landforms were used as a case study. The Machair ecosystem is a distinct and biodiverse coastal bio-type that includes all transient habitats from seaward embryo dunes to inland sand-affected peatlands, including low-lying, biodiverse grasslands listed on Annex I of the EC Habitats and Species Directive (Council Directive 92/43/EEC). Their distribution is confined globally to the north-western fringe of Europe (25000 ha) and while in Scotland (17500 ha) their extent is limited to the western and northern coasts, their distribution covers a latitudinal range of circa 650km. This gradient includes the transition from warmer, drier climes of the southern Inner Hebrides to the wetter, colder climes in the north. The plant communities of these Machair ecosystems have recently been described by Kent et al. (1996) and Dargie (1998).

5.2.2 Floristic and Environmental data

The Scottish Coastal Survey of 1975 to 1977 (Shaw et al. 1983), and a re-survey in 2009 to 2010 formed the data for this study. Percentage cover abundance of all occurring vascular plant species in 5 m x 5 m quadrats were recorded across almost the entire soft coast resource of Scotland. Re-survey methodology followed the original survey techniques of Shaw et al. 1983. Original plot coordinates (British National Grid) were relocated to within ± 10m accuracy using a hand held global positioning system. The final location of the plot was selected using information from the original vegetation composition to ensure that spurious changes due to relocation error were minimised. Where there was uncertainty over the original plot location, it was omitted from the re-survey. This method of revisitation surveying for non-permanent vegetation sampling has been shown to be effective in detecting temporal change with confidence (Ross et al. 2010).

For analyses of species temporal turnover, data were extracted forming a subsample of 46 sites (1322 plots) known to include Machair and its associated landforms and also for which climatic data were available (Fig. 5.1).

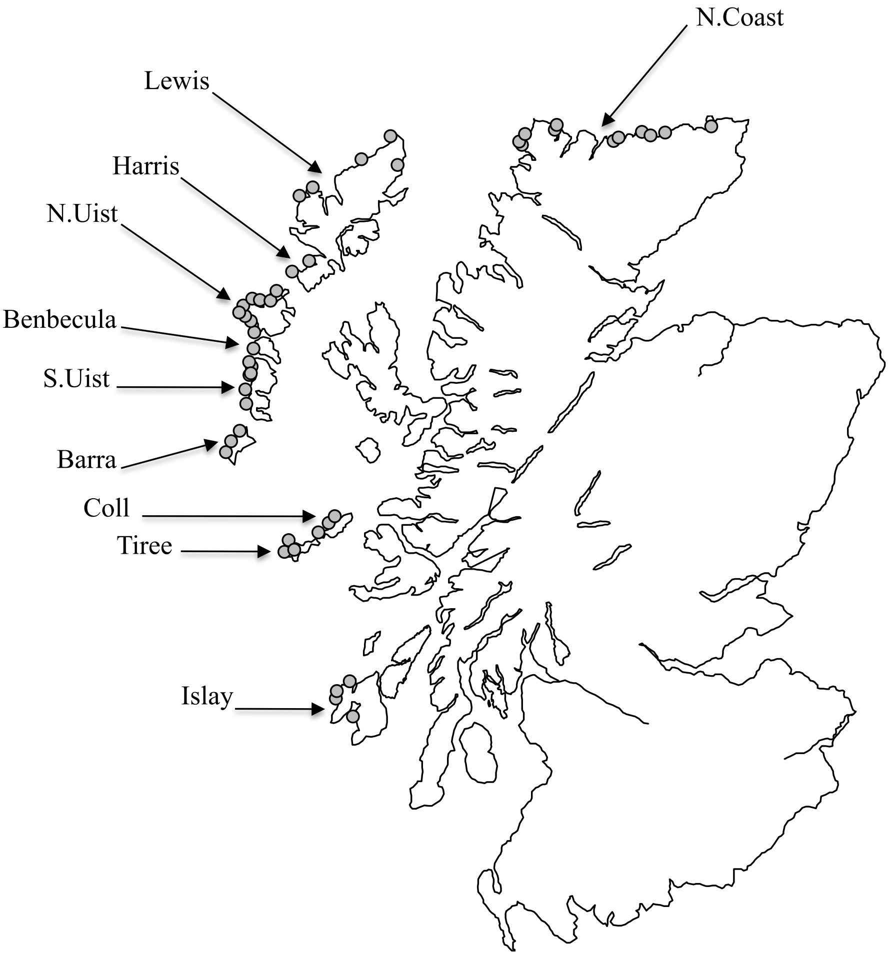


Fig. 5.1 Location of Machair grassland study sites throughout Scotland selected for turnover analyses.

The potential climatic drivers of β-diversity were represented by three variables that represent key aspects of climate driven macro-ecological variation. These were:

i. Water balance (drought) - calculated by subtracting total annual precipitation from potential evapotranspiration, using the method of Burt and Shahgedanova (1998). All negative values were set to zero to represent no water balance deficit.
ii. Annual mean minimum temperature (MinT); taken as the mean of the daily minimum temperature for the coldest month in each year.
iii. Growing degree days (GDD), expressed as the total accumulated temperature across every day of the year above a threshold of 5.5 Celsius.

Temperature and precipitation data were downscaled from 5 km gridded monthly data covering the period 1960 to 2000, obtained from the UK Meteorological Office [http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/].

These three climatic measures were expressed as five different measures following Lennon et al. (in prep.):

i. Mean: The sample mean was calculated (without detrending).
ii. Variance: The sample variance was calculated after detrending, as outlined in iii below.
iii. Long-term Trend: This is the rate of change of the variable along a timescale. Calculated by fitting a simple trendline using ordinary least squares regression to each 30-year time series and using the regression coefficient as the measure of the long-term trend.
iv. Short term predictability (autocorrelation): The correlation in values between consecutive pairs of years (the lag-1 autocorrelation coefficient) was calculated. The variables were first detrended by simple regression, as described above for Long-term Trend. The autocorrelation coefficient was extracted from the residuals.
v. Fat tail measure (extremity): This measure is a ratio of quantile differences (Q 0.975 – Q 0.025) / (Q 0.875 – Q 0.125) namely the time the climatic (or other) variable spends in a portion of either tail (the numerator) relative to the time it spends in the central part of its distribution (the denominator) (Schmid and Trede 2003). This measure was centred by subtracting a constant given by the value expected from a normal distribution (1.7038).

5.2.3 *Measuring beta diversity*

Following Lennon et al. (2001) notation for two sites (*i* and *j*), where *a* is the number of species common to both sites, *b* is the number of species unique to *i*, while *c* is the number of species unique to *j*, four different β-diversity indices were calculated for analysis, all of which quantified different components of β-diversity for the coastal vegetation assemblages.

The first of these was the Sørensen dissimilarity index (β_{sor}; Sørensen 1948), a widely used index of β-diversity:

$$\beta_{sor} = \frac{b+c}{2a+b+c} \qquad \text{(eqn 1)}$$

This index is a broad-sense measure of β-diversity (Koleff et al. 2003), in that it includes richness gradients as well as strict compositional differences.

In order to partition the fundamental components of species turnover (i.e. richness and replacement) two further indices were calculated. The index beta-gl (β_{gl}), an extreme broad-sense index, was applied to account only for patterns in local species richness gradients, independent of replacement mechanisms:

$$\beta_{gl} = \frac{2|b-c|}{2a+b+c} \qquad \text{(eqn 2)}$$

β_{gl} is insensitive to species replacement processes, and thus accounts only for species richness gradients driving β-diversity. Similarly, in order to account only for patterns in species replacement processes, independent of richness gradients, an extreme narrow-sense index β_{sim} (Simpson 1943; Lennon et al. 2001) was also calculated:

$$\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)} \qquad \text{(eqn 3)}$$

These two indices together roughly capture temporal turnover as the index β_{sor} , i.e. $\beta_{sor} \approx \beta_{gl} + \beta_{sim}$ (Lennon et al. 2001).

Finally a fourth measure was included to extend the identities of species to include relative abundance. Abundance information is an important aspect of community structure, and can yield useful insights when analysing change in community variation (Anderson et al. 2011). Here the Bray-Curtis index (Bray and Curtis 1957) was used, calculated as:

$$BC_{ij} = 100 - \left\{ 1 - \frac{\sum_{k=1}^{p} \left| Y_{ki} - Y_{kj} \right|}{\sum_{k=1}^{p} \left(Y_{ki} - Y_{kj} \right)} \right\} \qquad \text{(eqn 4)}$$

where Y_{ki} *and* Y_{kj} represent measures of species *k* in sites *i* and *j*, where *p* is the total number of species. The use of this index on non-standardised data gives emphasis to common and numerically dominant species. Therefore, before calculating equation 4, the species abundance matrix was standardised using the Wisconsin double standardization (Bray and Curtis 1957), a non-affine transformation that considers absolute differences to capture patterns of community structure.

These four indices were calculated for temporal turnover, i.e. β-diversity in time where sites *i* and *j* refer to the same site at two points in time and also to calculate spatial turnover, i.e. β-diversity in space where sites *i* and *j* refer to neighbouring sites in space. Spatial turnover was used as a model covariate in the multiple-regression to investigate spatial-temporal relationships. Spatial β-diversity measures were the means of pairwise values calculated from the focal site and each neighbouring site within a 5km radius. All β-diversity measures were calculated in R version 2.11.0 (R Development Core Team 2011), using the 'betadiver' (equations 1-3) and 'vegdist' (eqn 4) in the R package 'vegan' (Oksanen et al. 2011). Finally, in addition to spatial-turnover, longitude and latitude were introduced to some models to act as proxies for large-scale gradients in temporal turnover.

5.2.4 Model selection and significance testing

A multi-model inference approach (Burnham and Anderson 2002) was used to evaluate evidence for the stated hypotheses. In all cases, the objective was to explain the variation in temporal turnover. Therefore, for each metric of β-diversity, separate statistical models were fitted, where temporal β-diversity was the response variable and the five climatic measures based on MinT, drought and GDD as explanatory covariates; these were included as various subsets in the models in accordance with the hypotheses. These models also fell into four group sets depending on whether or not spatial coordinates and/or spatial turnover as additional covariates were included (Table 5.1).

To deal with the potential difficulties caused by residual spatial autocorrelation (Cressie 1993; Legendre 1993; Lennon 2000; Fortin and Dale 2005; Beale et al. 2010), generalised least squares models with exponentially spatially structured random effects (residuals) were used.

Table 5.1. Inclusion of longitude (x), latitude (y) and spatial turnover (β-space) as spatial covariates for Model Sets 1-4.

Model-Set	Regression Model
1	β-time~Climatic covariates+ x+y+β-space
2	β-time~Climatic covariates+ x+y
3	β-time~Climatic covariates+ β-space
4	β-time~Climatic covariates

For each model set, 25 models with differing combinations of climatic covariates were tested (Table 5.2). One model (M25) had only the intercept. The standard regression coefficient, p-value and pseudo r-square (square of the correlation of observed and predicted values) were recorded for each model. The most parsimonious model was identified using Akaike's Information Criterion (AIC; Burnham and Anderson 2002), the best being the model with the lowest AIC value in each set. To assess positive or negative associations of climatic model covariates with temporal turnover, average coefficients for each climatic measure were also calculated, (coefficients weighted by the Akaike weights). All statistical analyses were done in R version 2.11.0 (R Development Core Team (2011), using the 'gls' function in the R package 'nlme' (Pinheiro et al. 2011).

5.3 Results

Results suggest the hypotheses relating measured climatic variables to temporal turnover were not supported for all climatic measures tested, or across all metrics of β-diversity. Nonetheless, strong generalities did occur, some of which were in-line with our expectations.

Table 5.2 Combinations of climatic covariates fitted for models 1 to 25. Climatic attributes included are indicated by the shaded cells in the matrix. Modelled are the mean, variance, autocorrelation, slope and fat-tail of minimum temperature (T), water balance (D) and growing degree days (G).

		Model Covariates														
		Mean			Variance (var)			Auto-correlation (acf)			Slope (sl)			Fat-Tail (ft)		
Model	Covars	*x*T	*x*D	*x*G	varT	varD	varG	acfT	acfD	acfG	slT	slD	slG	ftT	ftD	ftG
M1	15	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
M2	12				■	■	■	■	■	■	■	■	■	■	■	■
M3	12	■	■	■				■	■	■	■	■	■	■	■	■
M4	12	■	■	■	■	■	■				■	■	■	■	■	■
M5	12	■	■	■	■	■	■	■	■	■				■	■	■
M6	12	■	■	■	■	■	■	■	■	■	■	■	■			
M7	6	■	■	■	■	■	■									
M8	6	■	■	■				■	■	■						
M9	6	■	■	■							■	■	■			
M10	6	■	■	■										■	■	■
M11	6				■	■	■	■	■	■						
M12	6				■	■	■				■	■	■			
M13	6				■	■	■							■	■	■
M14	6							■	■	■	■	■	■			
M15	6							■	■	■				■	■	■
M16	6										■	■	■	■	■	■
M17	3	■	■	■												
M18	3				■	■	■									
M19	3							■	■	■						
M20	3										■	■	■			
M21	3													■	■	■
M22	5	■			■			■			■			■		
M23	5		■			■			■			■			■	
M24	5			■			■			■			■			■
M25	0															

5.3.1 Significance of climatic covariates

Irrespective of the metric used to model β-diversity, extremely small Akaike weights (W_i) were found for the intercept only models (M25; Table 5.3). This suggests that the measured components of climate significantly influence temporal turnover. Comparison of the pseudo R^2's for models which include only climatic covariates (Model Set 4; Table 5.3) identified β_{gl} (pseudo R^2 = 0.07) as capturing more variability in the data than β_{sim} ,β_{sor} or β_{BC} (pseudo R^2's = 0.05).

5.3.1.1 Climatic means

Climatic means were only included in the most parsimonious model, where β-diversity was measured as β_{sim} (S3M9; Table 5.4). Here, only MinT was found to be significant ($p < 0.05$; Table 5.4), negatively influencing species temporal turnover (Fig. 5.2c). Mean covariates were, however, included in all second-best models determined by Akaike weights, irrespective of index used to measure β-diversity. With the exception of β_{BC}, (S1M6 W_i = 0.04, ΔAIC = 6.52; Table 5.3), evidence ratios (i.e. $w_1/w_2 = e^{(\Delta AIC/2)}$) were less than 2.5, which suggested little difference in parsimony between the best and second best models (Burnham and Anderson 2002). Nevertheless, significant covariates were shown only among the metric β_{gl} where MinT ($p < 0.05$; Table 5.4) was found to positively influence species temporal turnover (Fig. 5.2b), in contrast to the models for β_{sim} (Fig. 5.2c).

5.3.1.2 Climatic variance

Climatic variances were included in the best model where β-diversity was measured as the broad sense metric β_{sor} and the relative abundance measure β_{BC} (Table 5.4). For β_{sor} (W_i = 0.42*)*, GDD was the only significant variance covariate ($p < 0.01$; Table 5.4), and was positive as hypothesised (see H2). Similarly, the same was found for variance in drought ($p < 0.001$) for the best β_{BC} model (W_i = 0.92; Fig. 5.2d). However, contrary to expectations, the variance covariate of MinT, also within the best β_{BC} model was negatively associated with temporal turnover (Fig. 5.2d).

5.3.1.3 Climatic long-term trends

Independent of the index used to model β-diversity, models where long-term trend covariates were excluded had extremely small Akaike weights (Appendix 5.1-5.4). Moreover, results show parsimonious models all include long-term trend covariates (Table 5.4).

In the introduction it was hypothesised for long-term trends to be positively correlated with species temporal turnover (H3), but patterns identified among the weighted mean model coefficients do not support this across all the climatic variables measured. For example, where β-diversity was measured as β_{sor} and β_{gl}, MinT was negatively associated with species temporal turnover (Figures 5.2a & 5.2b).

Conversely, where β-diversity was measured as β_{sim} and β_{BC}, MinT was positively associated with species temporal turnover (Figures 5.2c & 5.2d). Furthermore, it is difficult to support one pattern over another, because model weights, particularly model group weights ($W_{i(g)}$) (i.e. weights taken within groups of models which express the same pattern of covariate exclusion) were greatest among two metrics displaying contrasting patterns with temporal turnover: MinT for β_{gl} ($W_{i(g)}$ =0.95; Table 5.3) showed a negative association with species temporal turnover, while for β_{BC} ($W_{i(g)}$ = 0.98; Table 5.3) MinT showed a positive association (Figures 5.2b & 5.2d).

In contrast to the above findings for MinT, patterns identified among the weighted mean model coefficients for the water balance covariate (drought) fully support the expectation (H3) that long-term trends in climate are associated positively with species temporal turnover (Fig. 5.2). Furthermore, with the exception of β_{sim}, the long-term trend in drought was shown to be a statistically significant model covariate ($p < 0.05$).

5.3.1.4 Climatic autocorrelation

Between-year similarity measures (i.e. autocorrelation) were only included in the best model where temporal turnover was measured as β_{sor} (Table 5.4). Here, only the autocorrelation of GDU was statistically significant ($p < 0.01$) among both the best (W_i = 0.43) and second best (W_i = 0.29) models (Table 5.3). Weighted mean model coefficients identified this measure to be negatively correlated with temporal turnover (Fig. 5.2a), as expected (see H4).

5.3.1.5 Climatic extremes

Measures of time spent in relatively unusual climatic space (i.e. fat-tail measure) were absent from the best models of turnover measured with β_{sim} and β_{BC} but present in the best models for β_{gl} and β_{sor}, although the covariates were not statistically significant for the latter (Table 5.4). For β_{gl}, MinT and water balance were statistically significant model covariates. Weighted mean model coefficients of significant fat-tail measures suggest a positive (MinT) and negative (drought) correlation with temporal turnover (Fig. 5.2b). Patterns across the remaining metrics of β-diversity for climatic extreme covariates were inconclusive.

Table 5.3 Model results from the general least squares analysis testing the models outlined in Tables 5.1 and 5.2. Presented are the best and second best models for each model set. The most parsimonious model for each metric of β-diversity identified as having the lowest AIC is denoted with ←.Delta AIC (Δ_{AIC}) and Akaike model weights (W_i and $W_{i(g)}$) are also shown. For results of all models see appendices 1-4.

Model Set		Model run		*pseudo* R^2	AIC	Δ_{AIC}	W_i	$W_{i(g)}$
β***Sor***:	Set 1	M6		0.29	-1547.88	0.00	0.34	0.40
		M2		0.29	-1547.09	0.79	0.23	0.27
		Intercept		0.23	-1498.40	49.48	6.15^{-12}	
	Set 2	M2		0.08	-1204.88	0.00	0.41	0.43
		M6		0.08	-1204.03	0.85	0.27	0.28
		Intercept		0.01	-1154.13	50.75	3.9^{-12}	
	Set 3	M2	←	0.29	-1550.02	0.00	0.42	0.43
		M3		0.29	-1449.26	0.77	0.29	0.30
		Intercept		0.21	-1480.85	69.17	4.01^{-16}	
	Set 4	M23		0.05	-1188.36	0.00	0.58	0.99
		M3		0.06	-1185.04	3.32	0.11	0.52
		Intercept			-1152.35	36.01	8.89^{-09}	
β***gl***:	Set 1	M6		0.10	4416.80	0.00	0.31	0.50
		M16		0.09	4417.61	0.82	0.20	0.54
		Intercept		0.06	4451.23	34.43	1.02^{-08}	
	Set 2	M6		0.08	4446.72	0.00	0.26	0.50
		M14		0.07	4447.77	1.05	0.16	0.36
		Intercept		0.04	4468.88	22.16	4.04^{-06}	
	Set 3	M16	←	0.09	4413.63	0.00	0.50	0.95
		M6		0.10	4415.89	2.26	0.16	0.35
		Intercept		0.01	4494.04	80.41	1.74^{-18}	
	Set 4	M16		0.07	4446.14	0.00	0.29	0.48
		M7		0.07	4446.57	0.43	0.24	0.39
		Intercept			4505.06	58.92	4.69^{-14}	
β***sim***:	Set 1	M9		0.12	3724.39	0.00	0.18	0.36
		M7		0.12	3725.14	0.75	0.12	0.25
		Intercept		0.10	3734.51	10.12	1.1^{-03}	
	Set 2	M6		0.06	3830.43	0.00	0.48	0.53
		M4		0.05	3832.62	2.19	0.16	0.53
		Intercept		0.002	3868.16	37.74	3.04^{-09}	
	Set 3	M9	←	0.12	3722.93	0.00	0.34	0.56
		M7		0.12	3724.73	1.80	0.14	0.23
		Intercept		0.09	3743.05	20.12	1.45^{-05}	
	Set 4	M3		0.05	3836.11	0.00	0.66	0.73
		M6		0.04	3840.20	4.10	0.09	0.09
		Intercept			3867.39	31.28	1.07^{-07}	
β***BC***:	Set 1	M12	←	0.11	2799.15	0.00	0.92	0.98
		M6		0.11	2805.67	6.52	0.04	0.57
		Intercept		0.07	2825.65	26.5	1.6^{-06}	
	Set 2	M12		0.08	2848.09	0.00	0.38	0.99
		M6		0.09	2848.67	0.57	0.29	0.46
		Intercept		0.02	2896.08	47.99	1.4^{-11}	
	Set 3	M23		0.09	2807.50	0.00	0.49	0.99
		M9		0.09	2810.01	2.51	0.14	0.39
		Intercept		0.06	2832.39	24.89	1.9^{-06}	
	Set 4	M8		0.05	2870.41	0.00	0.49	0.94
		M6		0.06	2872.89	2.47	0.14	0.39
		Intercept			2904.98	34.56	1.5^{-08}	

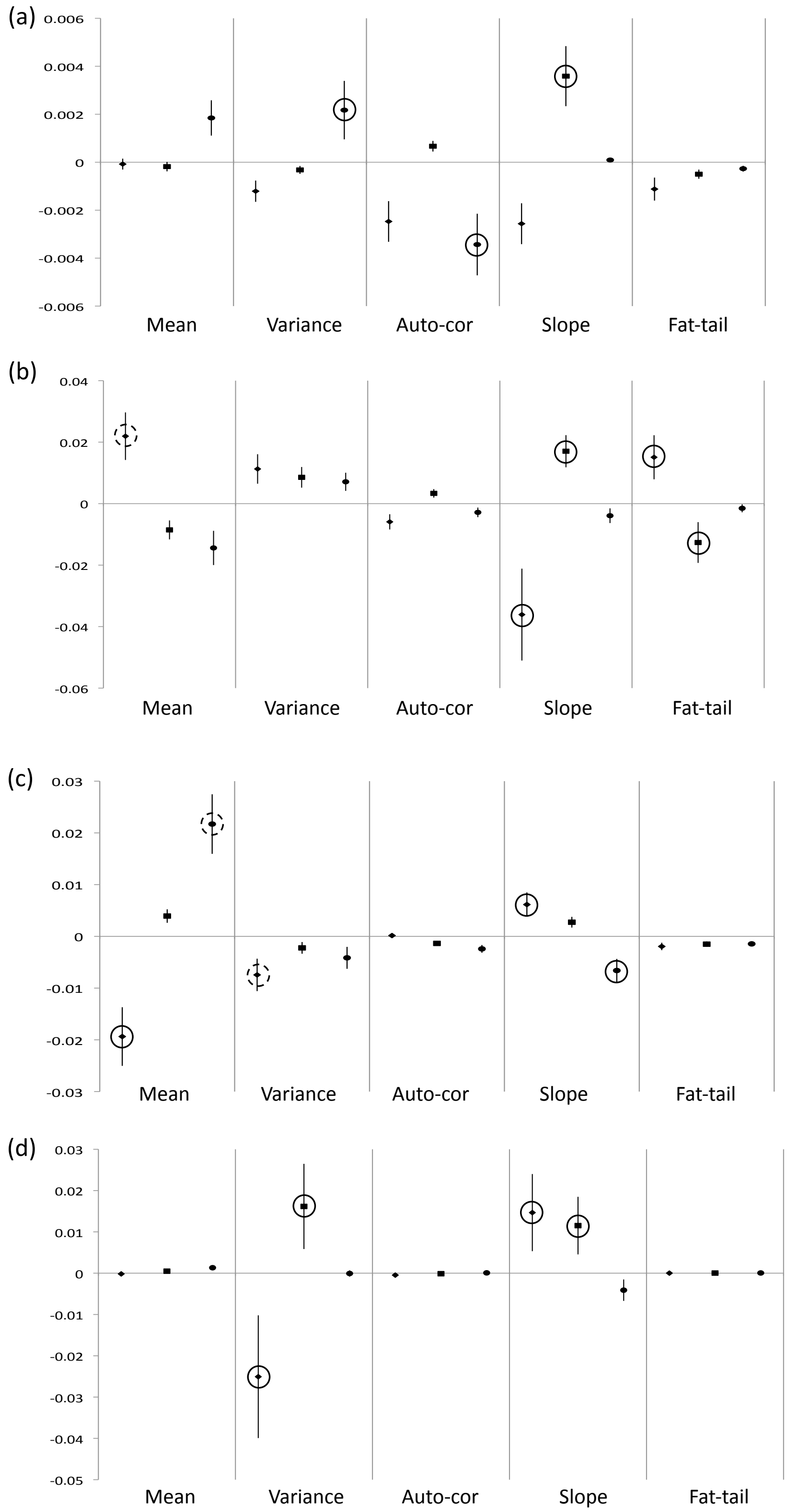


Fig. 5.2 Plots of model weighted correlation coefficients of minimum temperature [◆], drought [■], and growing degree units [●], for (a) β_{sor}, (b) β_{gl}, (c) β_{sim}, and (d) β_{BC}. Solid and dashed rings indicate significant climatic covariates among the best and second best model respectively, as identified by AIC.

5.3.2 Significance of spatial covariates

5.3.2.1 Spatial turnover

Models which included spatial turnover as a model covariate (i.e. models within Sets 1 & 3) displayed consistently lower AIC values compared to those that excluded spatial turnover. Therefore, irrespective of the β-diversity index used, the best models all included spatial turnover. Furthermore, spatial turnover was consistently significant ($p < 0.001$) across all presence/absence and the relative abundance dissimilarity indices. This clearly shows that spatial turnover is an important explanatory correlate of temporal turnover in the vegetation assemblages examined. This is further supported by the 'intercept only' models of model Sets 2 and 3 (Table 5.3). Here, pseudo R^2 values for models excluding spatial turnover (Set 2) ranged between 0.002 and 0.04, whereas those including only spatial turnover as a spatial covariate ranged between 0.01 and 0.23. It is noteworthy that spatial turnover measured as β_{gl} accounted for very little variability in the data in comparison with β_{sim}, β_{sor} and β_{BC} (Table 5.4).

5.3.2.2 Latitude and Longitude

Latitude and longitude as covariates act as proxies for very large-scale spatial gradients in temporal turnover attributable to unknown factors. Results for indices measuring presence/absence dissimilarity (i.e. β_{sor}, β_{gl}, β_{sim}) showed latitude and longitude to be poor explanatory covariates of temporal turnover; the best models were found within model Set 3, which excludes geographic coordinates. Contrary to the patterns displayed for the presence/absence metrics, model results from the Bray-Curtis dissimilarity measure showed longitude ($p < 0.001$) and latitude ($p < 0.05$) to be significant explanatory covariates of species relative abundance dissimilarity despite relatively small model coefficients (Table 5.4).

5.3.3 Beta diversity indices

Models for Sorønsens index (β_{sor}), were found to have the largest pseudo *R-square* (pseudo R^2 = 0.29); in comparison β_{gl} had pseudo R^2 = 0.09 and β_{sim} pseudo R^2 = 0.12. Contrary to expectation (H6), the models for which turnover was measured using species relative abundance information (β_{BC}), were not found to capture the most variation in the data compared to those for presence/absence metrics (pseudo R^2 = 0.11). These results therefore suggest that variation in the environmental data explains turnover as β_{sor} better than it does β_{sim}, β_{gl} or β_{BC}. This is perhaps not unsurprising given that β_{sor} measures both species richness gradients and species replacement, although it is unexpected for β_{BC}, given that abundance greatly extends species compositional information.

Table 5.4 Model coefficients of the two best approximating models for each index of temporal turnover in Scottish Machair grasslands. Five components of climate are presented: mean *(x),* variance (var), between year similarity (acf), long-term trend (sl), and climatic extremes (ft) for three climatic variables minimum temperature (T), water balance (D) and growing degree days (G). Spatial covariates include longitude (Long) and latitude (Lat) and spatial turnover (β-Space). All coefficients have been multiplied by 10. Significant model coefficients are in **bold**. **'**, $p < 0.05$; **''**, $p < 0.01$; **'''**, $p < 0.001$

	Model	Long	Lat	*x*T	*x*D	*x*G	varT	varD	varG	acfT	acfD	acfG	slT	slD	slG	ftT	ftD	ftG	β-Space
β_{sor}	S3M2						-0.11	-0.03	**0.48''**	-0.28	0.06	**-0.44''**	-0.27	**0.42'''**	0.01	-0.17	-0.06	-0.04	**7.94'''**
	S3M3			0.08	-0.1	0.37				-0.21	0.08	**-0.37''**	-0.24	**0.35'''**	-0.01	-0.1	-0.08	-0.03	**7.93'''**
β_{gl}	S3M16												**-4.8'''**	**1.3'**	-0.7	**2.3''**	**-2.2'''**	-0.4	**14.2'''**
	S3M6			**4.9'**	-2.2	-3.2	2.4	1.9	2.9	-1.8	1.2	-1.6	-2.3	**3.2'''**	0.4				**14.5'''**
β_{sim}	S3M9			**-2.0'**	0.1	1.9							**1.1'**	0.5	**-1.0'**				**31.1'''**
	S3M7			**-3.9''**	1.0	**4.7'''**	**-3.3'''**	-0.5	-1.9										**31.4'''**
β_{BC}	S1M12	**0.06'''**	**-0.02'**				**-2.68''**	**1.86'''**	0.11				**1.69''**	**1.26''**	-0.47				**18.4'''**
	S1M6	**0.07'''**	**-0.02'**	-0.54	1.0	2.41	**-4.62''**	0.61	-1.85	-1.02	-0.25	0.17	0.65	**1.53''**	-0.29				**18.5'''**

5.4 Discussion

This study found temporal turnover patterns in plant diversity to be significantly associated with climatic variation. Although the total variation explained by climatic measures was low across all metrics of turnover (ca. 5-7%), Akaike weights for models, including climatic covariates, were much greater than those where climatic covariates were excluded (i.e. *intercept models*). This suggests that variation in climate over the studied time-scale has had a relatively small yet significant influence on the temporal patterns of Scottish Machair vegetation.

5.4.1 Climatic component

Unlike most studies investigating temporal turnover, this study used multiple measures for quantifying spatial and temporal turnover. One of the objectives for using this approach was to attempt to separate out the effects of climate on species richness differences (β-diversity caused by species loss or gain) and species compositional differences (β-diversity caused by species replacement), using a suite of presence/absence measures that represented a narrow (β_{sim}) to broad (β_{gl}) spectrum of turnover (Lennon et al. 2001). Here, several simple hypotheses regarding the response of temporal turnover to various aspects of climate were tested. The response was expected to be consistent regardless of the measure of turnover used; however contrasting responses between the richness and replacement processes of turnover were shown. This was most evident for long-term trends in minimum temperature (MinT), a significant model covariate for temporal turnover measured as β_{gl} and β_{sim}. Here, there was a negative association with β_{gl} contrasting with a positive one for β_{sim} (Figures 5.2b & 5.2c). Such patterns suggest that steeper rates of temperature change (here MinT) promote species replacement processes while reducing species richness gradients, that is, compositional change that in turn dampens changes in species richness.

Much of Scottish Machair, particularly that of the Outer Hebrides is restricted to regions with hyper-oceanic climatic conditions, where humidity, wind speeds and precipitation are high and annual temperate range is low. The climate is, in part, responsible for increasing the biodiversity value of these regions, as the competitive ability of species common to low-lying grasslands are suppressed under a hyper-oceanic climate permitting less competitive species to persist (Averis et al. 2000). Therefore it is possible for any relaxation among the climatic environment to favour widespread generalists, replacing previously distinct vegetation communities containing specialists for ones with greater compositional similarity and lower biodiversity. Steepest gradients in temperate change are reported for regions of the Outer Hebrides; greatest for the islands of Harris and Lewis (Fig. 5.3a), for which large reductions in both α- and β-diversity were found (Table. S5.1).

Results therefore lend support to concerns raised of biotic homogenisation for these islands, as discussed in Chapter 3, where a significant decline in species indicative of high-quality Machair was identified. Given the small proportion of total variation explained, it seems unlikely that trends in climate are the sole driving force of such temporal vegetation change. However, factoring in changes in land use management reported for these regions (Pakeman et al. 2011) may provide a more complete explanation (McKinney and Lockwood 1999, Smart et al. 2006). Nonetheless, it remains likely that climatic variation and long-term change can contribute towards accelerated biodiversity loss in these human-modified ecosystems.

The only consistent climatic covariate across all measures of turnover was that of water balance trends (slD). This covariate showed a positive association with temporal turnover, matching model expectations (H3). Further, models showed slD to be a statistically-significant model covariate for all presence/absence measures of turnover.

Figure 5.3b illustrates where the long-term rate of change in water balance is steepest (i.e. South Uist and the Inner Hebrides: Coll, Tiree & Islay). This pattern correlates well with regions displaying the steepest temporal species richness gradients, as measured using β_{gl} (Fig. 5.4b; Table S5.1).

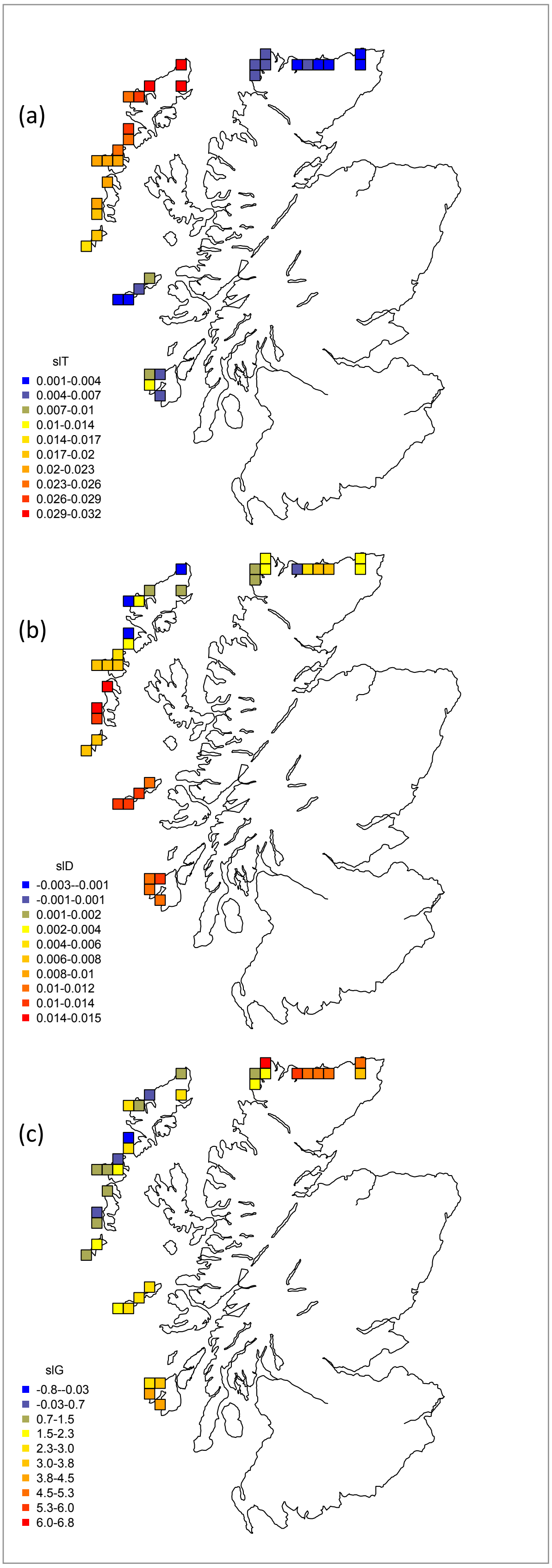


Fig. 5.3 Spatial patterns of the slope of climatic long-term trends for Scottish coastal areas between 1960 - 2000 for **(a)** mean minimum temperature (MinT), **(b)** water balance (drought) and **(c)** growing degree days (GDD).

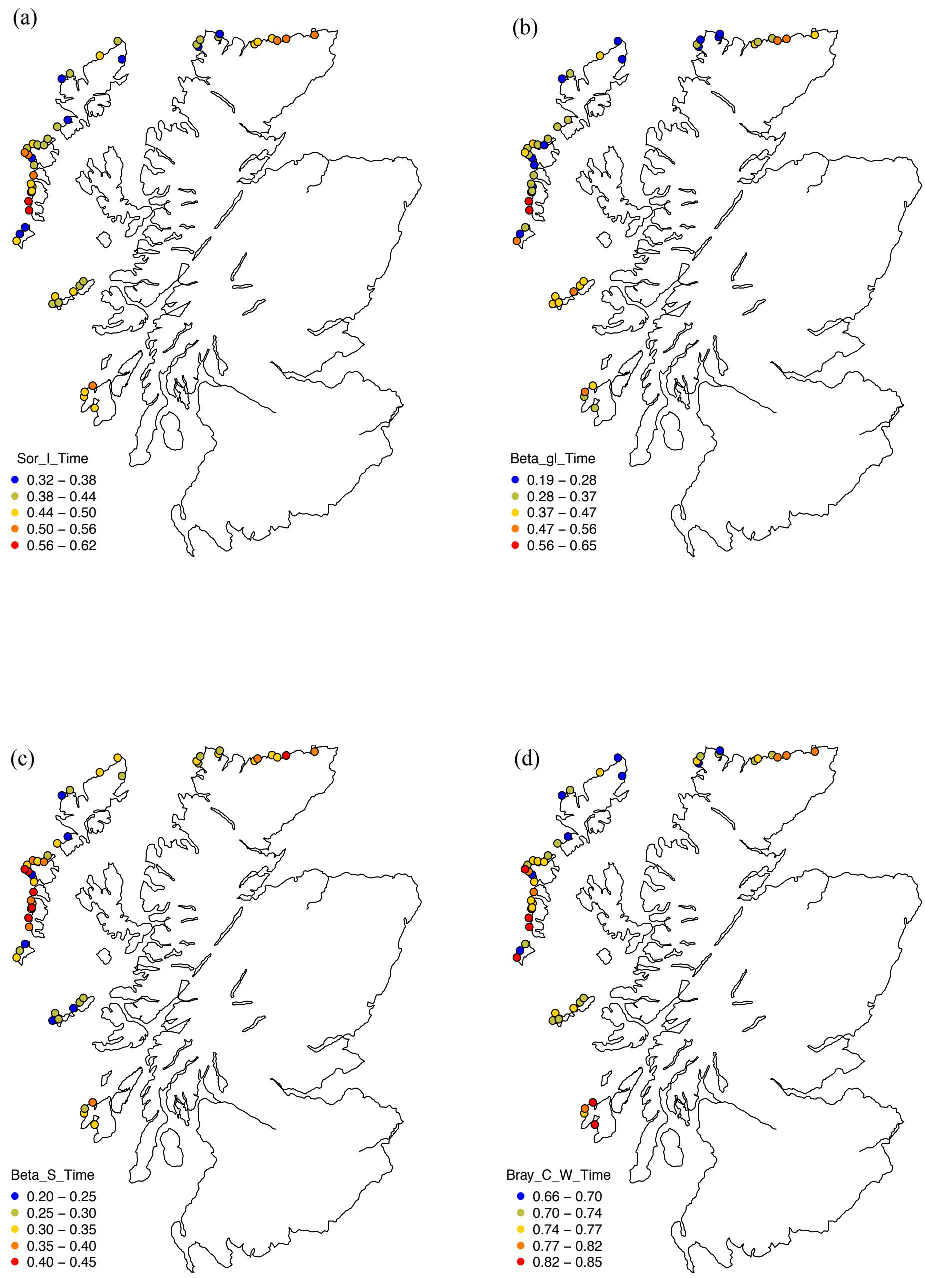


Fig. 5.4 Rate of temporal turnover, mapped for **(a)** β_{sor}, **(b)** β_{gl}, **(c)** β_{sim} and **(d)** β_{BC}.

Therefore, results suggest biodiversity change for these more southerly sites may potentially result from short-term droughts, impacting on local species recruitment and extinction processes. Given the relatively low water holding capacity of Machair grassland soils, even relatively weak gains in drought measures may affect Machair grasslands to a greater extent compared to other semi-natural grassland with a different substrate. Ecosystems under stress through resource constraints, such as water stress, can increase the probability of successful species colonisation by reducing the prevalence and competitive interactions of dominant species (Bartha et al. 2003). It is possible to then explain why the richness difference for these regions is representative of species gain (Table S5.1). However, given the strong connection between biodiversity of the Machair grasslands and land use (Angus 2001), it is equally plausible for changes in climate to impact on the way the land is managed. Extremely wet conditions, particularly high winter precipitation, can impact on the biodiversity of the Machairs, disrupting traditional management regimes that give rise to the high botanical diversity (Angus 2009). It may be that these regions, which already have the highest average minimum temperatures (Fig. S5.1a) and growing season (Fig. S5.1c), are increasingly subject to reduced rainfall and thus less likely to experience complications with winter grazing of cattle and delayed ploughing as a result of standing water late into the spring. Alternatively, increased summer drought may reduce the incentive to crop the Machair. In the short-term, this would see a rise in biodiversity as more land is effectively left as fallow. However in the long-term lack of agricultural use would be highly detrimental. Secondary effects of climate change on land use management are thus extremely important in light of knock-on effects on socio-economic change and current economic viability of traditional Machair management. Further pressures imposed through changing climate may further discourage traditional management that affects the biodiversity value of these regions (Angus and Hansom 2004) and may further account for the decline in biodiversity reported for Lewis, Harris and the North Coast, the only regions to report a decline in the water balance measure (Fig. 5.3b).

Variance measures were only included in the best models, where turnover was measured as β_{sor} and β_{BC}. Here, growing degree units (GDD; β_{sor}) and water balance (Drought; β_{BC}) were statistically significant, showing a positive relationship with temporal turnover. Similarly a positive variance-turnover relationship was repeatedly shown for all climatic variance measures modelled using β_{gl}, as predicted by Hypothesis 2. However, in contrast, negative variance-turnover relationships were found for minimum temperature (MinT) for the best (β_{BC}) and second best (β_{sim} ΔAIC = 1.8) models. This is probably a reflection of variance in MinT being at its lowest among the islands of the Outer Hebrides, (Fig. S5.2a), where temporal turnover measures through β_{sim} and β_{BC} were at their highest (Figures 5.4c & 5.4d). This lends more support for an increase in β-diversity with climatic variance through increased richness gradients rather than replacement processes. In fact β-diversity solely attributable to replacement processes actually declined with increasing climatic variation, whereas patterns of percentage compositional dissimilarity were found to fluctuate depending on the climatic covariate.

Because environmental dissimilarity (variance) was expected to increase temporal turnover (H2), it was also expected that evidence of climatic similarity would show the opposite effect (H4). However, only the broad-sense measure β_{sor} included auto-correlation covariates in the best models, identifying a statistically significant lag1 autocorrelation measure for GDD negatively associated with temporal turnover, as expected. Models for other β-diversity indices all revealed weak patterns of between-year similarity with temporal turnover.

Fat-tail measures, i.e. measures that identify how much time a site is subject to relatively unusual climatic conditions, were also relatively inconclusive for three of the four measures of turnover. The best model for the index β_{gl} included fat-tail measures, displaying MinT and water balance as significant model covariates. Results suggest that time spent in relatively unusual temperatures promotes the species richness component of temporal turnover significantly, while the same applied to water balance reduces the species richness component of temporal turnover significantly. Regions where fat-tail measures of minimum temperatures were greatest (Fig. S5.4a) were those areas showing declines in α- and γ-diversity (Table S5.1), indicating an adverse effect of time spent outside the normal temperature range on biodiversity. Similarly, the same regions, although here also including the North Coast, were shown to have the most time spent under relatively unusual water balance regimes (Fig. S5.4b).

5.4.2 Spatial turnover

Measures of spatial turnover were included in all parsimonious models irrespective of how turnover was calculated. A positive spatial-temporal-turnover relationship shown here is consistent with previous studies (Ptacnik et al. 2008; Ptacnik et al. 2010; Stegen et al. 2012) and conforms to the species-time-area-relationship (Alder et al. 2005; White et al. 2006), which suggests that spatial and temporal turnover are inextricably linked. Theory suggests that, if species are randomly placed throughout the landscape, increased temporal turnover will promote an increase in spatial turnover (Steiner and Leibold 2004). The present study focused solely on variation among different components of climate. Nevertheless, β-diversity in time is likely to be simultaneously driven by a variety of ecological and physical variables (Korhonen et al. 2010), all of which also influence the spatial heterogeneity of ecological communities. Quantification of β-diversity in space, as presented here, will almost certainly have captured some of this variation, owing to, for example: soil chemistry, land use or exposure, all of which strengthens the spatio-temporal turnover relationship. However, through comparison of the different measures of turnover, it is clear that the degree to which spatial turnover influences the different components of temporal turnover may not be uniform. The results suggest that spatial turnover has a stronger influence over the species replacement component than the species richness component, as the index sensitive to replacement processes captured much more variation when spatial turnover was the only modelled covariate. This pattern clearly warrants additional analyses.

5.4.3 Unexplained variation

The large fractions of unexplained variation in turnover were perhaps not surprising, given the national extent and relative fine-scale nature of this study. Spatio-temporal ecological datasets tend to be inherently noisy and it can be argued that the finer the spatial grain of the data, the greater the chance that temporal variation in species occurrence is subject to random, stochastic processes. Furthermore, the biodiversity of Machair grasslands are well documented to be directly linked to rotational arable agriculture. This form of low-intensity land use results in an extremely heterogeneous landscape of crops and variable-aged fallow grasslands, as well as dunes and permanent pasture. Although spatial turnover as measured here and analysed in the various models, is likely to have captured some of this between-quadrat variation, results from Chapter 2 suggest even the relatively fine-scale resolution of this national dataset is still too coarse to successfully capture most spatially-scaled management determinants of Machair grassland habitats.

5.4.4 Relative abundance measure

β-diversity metrics that include relative abundance information can give drastically different results to metrics that only include presence/absence information (Anderson et al. 2011). However, this study shows β-diversity measured using the relative abundance metric Bray-Curtis (pseudo R^2 = 0.11) to be poorly described by model covariates, in contrast to the presence/absence index (β_{sor}) that contains both richness and replacement components of turnover (pseudo R^2 = 0.29). These results are contrary to that predicted (H6). Nevertheless, the best model of β_{BC} captured similar proportions of variation in temporal turnover as β_{sim} (pseudo R^2 = 0.12), and even out-performed β_{gl} (pseudo R^2 = 0.09).

It is important that caution is expressed when interpreting pseudo R^2 values, as they are at best only an approximation of model performance and effect size. The substantial difference between pseudo R^2 for β_{sor} comparative to the other metrics is likely to be representative of the divergence in model performance explained between β_{sor} and the other presence and absence metrics, given that β_{sor} represents both components of turnover. However, given the relatively similar pseudo R^2 values of the best models calculated using turnover indices other than β_{sor}, discriminating between them is difficult, so making any inferences about the utility of one metric over another is avoided.

5.5 Conclusions

Climate has a small yet statistically significant role in governing vegetation patterns of Machair grasslands in time. This study found that the associations between different climatic components of change and temporal turnover do not always match expectations. Through utilising multiple indices to measure turnover, this study demonstrates how indices measuring separate components of turnover (richness gradients and species replacement), can show contrasting responses to different aspects of climatic variation; these patterns can be mixed when using an index that captures both components simultaneously. Furthermore, this study found little difference between turnover measures in terms of overall levels of temporal variation captured by climate but did find considerable differences in terms of temporal variation captured by the spatial component; β_{sor} captured far greater temporal variation through the spatial turnover covariate than any other index. The multi-index methods used here have the potential to provide greater insight into the processes that maintain biodiversity over similar approaches using only one index of turnover.

REFERENCES

Alder, P.B., White, E.P., Lauenroth, W.K., Kaufman, D.M., Rassweiler, A. and Rusak, J.A. 2005. Evidence for a general species-time-area relationship. Ecology 86, 2032-2039.

Anderson, M.J., Ellingsen, K.E. and McArdle, B.H. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9, 683-693.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D. et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14, 19-28.

Angus, S. 2009. Dé tha cearr air a'mhachaire? Biodiversity issues for Scottish Machair: an initial appraisal. The Glasgow Naturalist 25, Supplement. Machair Conservation: Successes and Challenges, 53-62.

Angus, S. and Hansom, J.D. 2004. Tir a' Mhachair, Tir nan Loch? Climate change scenarios for Scottish Machair Systems: A wet future? Proceedings Vol.2. Littoral 2004. Delivering sustainable coast: connecting science and policy. 565-569.

Averis, A.B.G, Averis, A.M., Horsfield, D. and Thompson, D.B.A. 2000. The upland vegetation of the Western Isles, Scotland. Scottish Natural Heritage. Research, Survey and Monitoring Report, No. 164.

Bartha, S., Meiners, S.J., Pickett, S.T.A. and Cadenasso, M.L. 2003. Plant colonization windows in a mesic old field succession. Applied Vegetation Science 6, 205-212.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134-143.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. et al. 2010. Regression analysis of spatial data. Ecology Letters 13, 246-264.

Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27, 325-349.

Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference. Springer, New York.

Burt, T.P. and Shahgedanova, M. 1998. An historical record of evaporation losses since 1815 calculated using long-term observations from the Radcliffe Meteorological Station, Oxford, England. Journal of Hydrology 205, 101-111

Carvalho, J.C., Cardoso, P. and Gomes, P. 2012. Determining the relative roles of species replacement and species richness difference in generating beta-diversity patterns. Global Ecology and Biogeography 21, 760-771.

Cressie, N.A.C. 1993. Statistics for spatial data. Wiley, New York.

Dargie, T.C.D. 1998. Sand dune vegetation survey of Scotland: Western Isles. Scottish Natural Heritage research survey and monitoring report No. 96, Scottish Natural Heritage, Battleby, Perth, UK.

Darwin, C. 1859. On the origin of species by means of natural selection. John Murray. London.

Díaz, S., Cabido, M. and Casanoves, F. 1998. Plant functional traits and environmental filters at the regional scale. Journal of Vegetation Science 9, 113-122.

Fortin, M. and Dale, M. 2005. Spatial analysis: a guide for ecologist. Cambridge University Press.

Holmgren, M., Scheffer, M., Ezcurra, E., Gutiérrez, J.R. and Mohren, G.M.J. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16, 89-94.

Huntley, B., Green, R.E., Collingham, Y.C. and Willis, S.G. 2007. A climatic atlas of European breeding birds. Lynx Edicions, Barcelona.

Huntley, B., Barnard, P., Altwegg, R., Chambers, L., Bernard, W.T. et al. 2010. Beyond climatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. Ecography 33, 487-516.

Juranski, G., Retzer, V. and Beierkuhnlein. C. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. Oecologia 159, 15-26.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3, 157-164.

Kent, M., Weaver, R.E., Gilbertson, D.D., Wathern, P. and Brayshay, B.A. 1996. The present-day machair vegetation of the southern Outer Hebrides. In Gilbertson, D., Kent, M. and Grattan, J. (eds.) The Outer Hebrides: the last 14,000 years, pp. 133-145. Sheffield Academic Press, Sheffield.

Koleff, P., Gaston, K.J. and Lennon, J.J. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72, 367-382.

Korhonen, J.J., Soininen, J. and Hillebrand, H. 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. Ecology 91, 508-517.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659-1673.

Legendre, P. and Legendre, L. 1998. Numerical ecology. 2nd ed Elsevier, Amsterdam.

Legendre, P., Borcard, D. and Peres-Neto, P.R. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75, 435-450.

Legendre, P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. Journal of Plant Ecology 1, 3-8.

Lennon, J.J. 2000. Red-shifts and red herrings in geographical ecology. Ecography 23, 101-113.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. and Gaston, K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. Journal of Animal Ecology 70, 966-979.

McKinney, M.L. and Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14, 450-453.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B. et al. 2011. vegan: Community Ecology Package. R package version 1.17-8. http://CRAN.R-project.org/package=vegan

Pakeman, R.J., Huband, S., Kriel, A. and Lewis, R.J. 2011. Changes in the Management of Scottish Machair Communities and Associated Habitats from the 1970s to the Present. Scottish Geographical Journal 127, 267-287.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and the R Development Core Team. (2011) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-102.

Podani, J. and Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence/absence data. Oikos 120, 1625-1638.

Polis, G.A., Hurd, S.D., Jackson, C.T. and Piñero, F.S. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology 78, 1884-1897.

Ptacnik, R., Solimini, A.G., Anderson, T., Tamminen, T., Brettum, P. et al. 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. Proceedings of the National Academy of Sciences 105, 5134-5138.

Ptacnik, R., Anderson, T., Brettum, P., Lepisto, L. and Willén, E. 2010. Regional species pools control community saturation in lake phytoplankton. Proceedings of the Royal Society B: Biological Sciences 277, 3755-3764.

Qian, H., Ricklefs, R.E. and White, P.S. 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. Ecology Letters 8, 15–22.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://cran.r-project.org/.

Ross, L.C., Woodin, S.J., Hester, A., Thompson, D.B.A. and Birks, H.J.B., 2010. How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? Plant Ecology and Diversity 3, 1-8.

Schmid, F. and Trede. M. 2003. Simple tests for peakedness, fat tails and leptokurtosis based on quantiles. Computational Statistics and Data Analysis 43, 1-12.

Shaw, M.W., Hewett, D.G. and Pizzey, J.M. 1983. Scottish coastal survey. Institute of Terrestrial Ecology. Bangor Research Station, Bangor, Gwynedd.

Simpson, G.G. 1943. Mammals and the nature of continents. American Journal of Science 241, 1-31.

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C. and Firbank, L.G. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. Proceedings of the Royal Society B 273, 2659-2665.

Sørensen, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Dannish commons. Kongelige Danske Videnskaernes Selskabs Biologiske Skrifter 5, 1-34.

Stegen, J.C., Freestone, A.L., Crist, T.O., Anderson, M.J., Chase, J.M. et al. 2012. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. Global Ecology and Biogeography, online.

Steiner, C.F. and Leibold, M.A. 2004. Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. Ecology 30, 3-12.

Svenning, J.C., Fløjgaard, C. and Baselga, A. 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. Journal of Animal Ecology 80, 393-402.

Tuomisto, H., Ruokolainen, K. and Yli-Halla, M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. Science 299, 241-244.

Tuomisto, H. and Ruokolainen, K. 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. Ecology 87, 2697-2708.

Tuomisto, H. 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining betat diversity as a function of alpha and gamma diversity. Ecography 33, 2-22.

Tuomisto, H. 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33, 23-45.

Wallace, A.R. 1870. Contribution to the theory of natural selection. Macmillan. London.

White, E.P., Alder, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D. et al. 2006. A comparison of the species-time relationship across ecosystems and taxonomic groups. Oikos 112, 185-195.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30, 279–338.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21, 213-251.

Appendices 5.1 – 5.4

Appendix 5.1, 5.2, 5.3 and 5.4 can be found in electronic format on the attached compact disk at the back of this thesis.

Model results from the general least squares analysis for all models (M1-M25; Table 5.2) for four models sets (Table 5.1) are displayed for β_{sor} (Appendix 5.1), β_{gl} (Appendix 5.2), β_{sim} (Appendix 5.3) and β_{BC} (Appendix 5.4). The most parsimonious model for each model set (identified as having the lowest AIC) is highlighted in grey. Delta AIC (Δ_{AIC}) and Akaike model weights (W_i and $W_{i(g)}$) are shown. Significance of model coefficients for each model are represented by **'**, $p < 0.05$; **''**, $p < 0.01$; **'''**, $p < 0.001$.

Supplementary Material (S5)

Table S5.1. Regional details, including: number of sites, number of 5 m x 5 m plots and alpha (α) and gamma (γ) diversity recorded for the two survey years.

	No.Sites	No.Plots	α^{1976}	α^{2010}	γ^{1976}	γ^{2010}
Barra	3	56	19.6	24.4	96	109
Benbecula	1	20	21.7	20.1	76	77
Coll	3	119	18.8	28.8	133	183
Harris	2	58	22.7	20.6	153	128
Islay	4	141	18.2	24.7	177	208
Lewis	5	121	27.5	26.2	181	161
N. Coast	11	252	27.7	25.7	291	260
N. Uist	8	259	25.6	24.9	233	212
S. Uist	6	193	20.6	25.6	214	238
Tiree	3	103	18.1	27.8	104	135

Supplementary Material (S5): Continued..

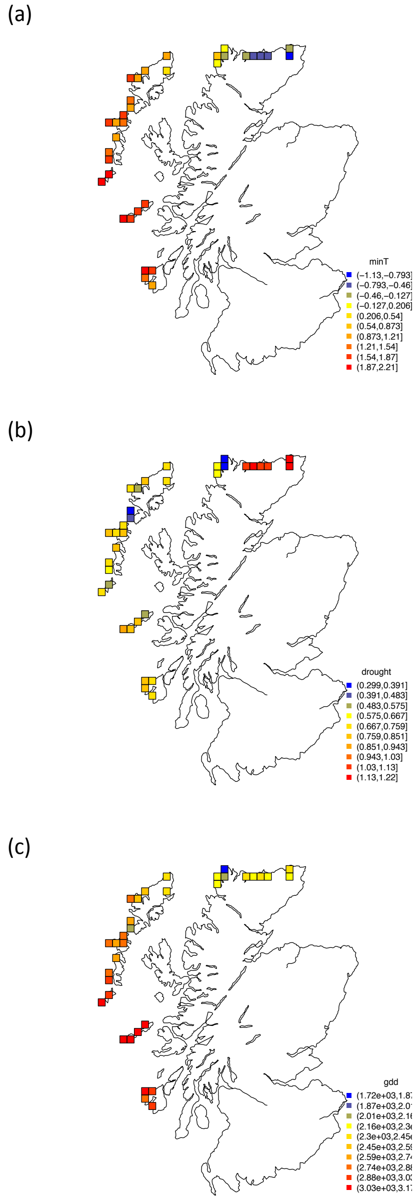


Fig. S5.1 Spatial patterns of climatic means change for Scottish coastal areas between 1960 - 2000 for **(a)** mean minimum temperature (MinT), **(b)** water balance (drought) and **(c)** growing degree days (GDD).

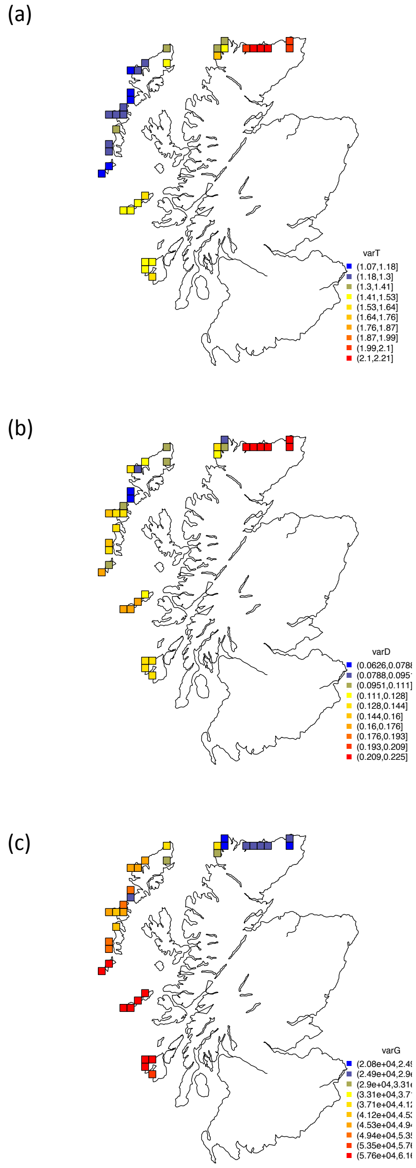


Fig. S5.2 Spatial patterns of climatic variance for Scottish coastal areas between 1960 - 2000 for **(a)** mean minimum temperature (MinT), **(b)** water balance (drought) and **(c)** growing degree days (GDD).

Supplementary Material (S5): Continued..

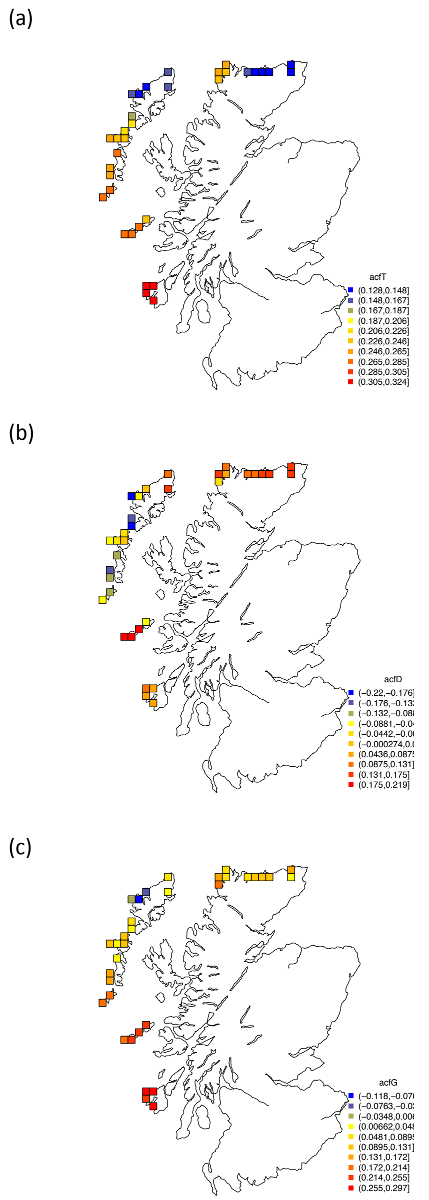


Fig. S5.3 Spatial patterns of between year climatic similarity for Scottish coastal areas between 1960 - 2000 for **(a)** mean minimum temperature (MinT), **(b)** water balance (drought) and **(c)** growing degree days (GDD).

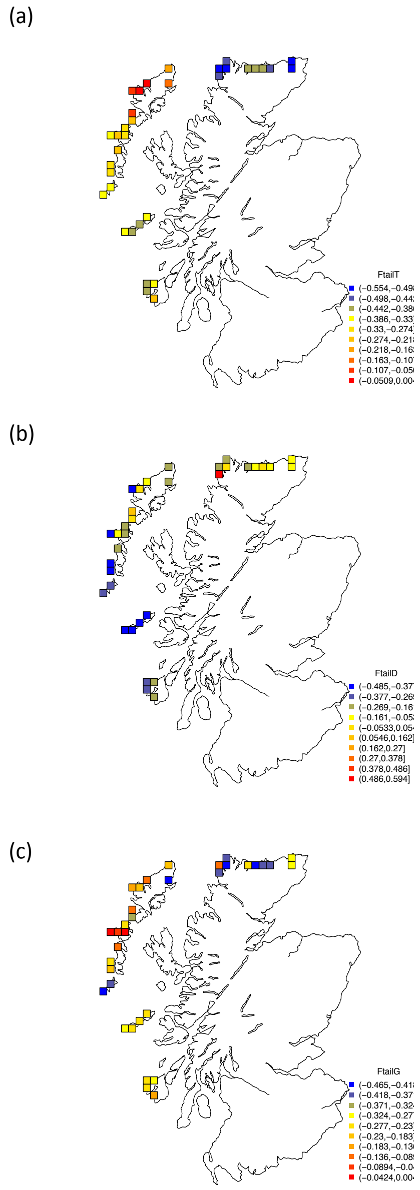


Fig. S5.4 Spatial patterns of time spent under relatively unusual climatic extremes for Scottish coastal areas between 1960 - 2000 for **(a)** mean minimum temperature (MinT), **(b)** water balance (drought) and **(c)** growing degree days (GDD).

Chapter Six

General Discussion

Making sense of spatial and temporal patterns among vegetation assemblages is vital for successful future biological conservation. Understanding the processes that maintain biodiversity allows for a better insight into how species and communities are likely to respond to future environmental change (e.g. Suding et al. 2008). This is of upmost importance, not solely for biological conservation, i.e. the protection of biodiversity, but also for ensuring the protection of ecosystems services i.e. natural services through which humans ultimately depend (e.g. carbon storage, food production, hydrology, nutrient cycling, etc). Nowhere is this need greater than for globally-rare, and threatened habitats, through which the relation between the environment and land use establishes high bio-diversity.

This thesis addresses a range of approaches for investigating spatial and temporal vegetation patterns. It focuses on the coastal grasslands of Scotland, particularly those of the western and northern seaboard termed 'Machair'. With a global extent of a mere 30,000-40,000 ha, of which over two thirds is found in Scotland (Dargie 2000; Anon. 2008), the protection of Machair grasslands is extremely important from both a UK national and an international conservation perspective. Renowned for their high botanical diversity, while also supporting rare and protected species of birds (*Carex carex; Milaria calandra*) and insects (*Bombus distinguendus*), the conservation value of Machair grasslands are strongly linked to forms of low-intensity agriculture, both pastoral and arable (Angus 2009). Socio-economic change, leading to shifts away from traditional forms of management to either abandonment or conversely more intensive methods of agriculture more typical of mainland UK and Europe is causing substantial conservation concern (Pakeman et al. 2011). This, coupled with added pressures of loss and degradation through sea-level rise and climatic change, means these habitats are extremely vulnerable (Angus et al. 2011) and consequently are protected under the European Habitat Directive 92/43/EEC (Council of European Commission 1992).

In order to assist effective management strategies for safeguarding this internationally important habitat, this thesis had a number of aims. The first was to assess the relative importance of land use and climate as drivers of spatial vegetation patterns of almost all Scotland's soft coast sites, inclusive of Machair and non-Machair coastal grasslands (Chapter 2), using an historic extant dataset. Further, methods capable of dissecting the spatial scale of environmental determinants were used to establish the scale at which land use and climatic drivers operate. The results were used to indicate the operation of different community assembly processes at different scales (Chapter 2). Second, following information gathered from an extensive re-survey of the original data, surveying sites known to include Machair, comparative analyses investigated the major temporal shifts in vegetation assemblages, with the aim of linking patterns of vegetation change to change in land use and or climate (Chapter 3). Similarly, the same was asked of change in species functional response traits and functional diversity, and whether temporal change in function diversity provided an insight into the community assembly processes governing Machair grasslands (Chapter 4). The final objective was to assess the relative importance of different measurable components of climate on the temporal turnover of these grasslands. A multi-index approach was used to assess different measurable components of spatial and temporal turnover. Spatial turnover was included in the models with climate to further investigate the importance of spatial turnover patterns in explaining temporal turnover patterns (Chapter 5). Specifically the work addressed the following questions, discussed in the numbered sections below:

- What is the relative importance of land use and climate as drivers of spatial vegetation patterns across Scotland's soft coasts? (Chapter 2).

- How are land use and climatic determinants of Scotland's soft coast spatially scaled, and what can this tell us about the community assembly processes that operate to govern the vegetation assemblages of these communities? (Chapter 2).

- What are the major shifts in plant species assemblages of the Machair system and Machair grassland over 30 years of change, and can changes in land use and climate be linked to changes in vegetation? (Chapter 3).

- Can temporal patterns of plant functional traits help to confirm observed and reported shifts away from traditional land use management among the Machair grasslands? (Chapter 4).

- Can functional trait diversity; measured using Richness, Divergence, Evenness and Dispersion indices help to identify how land use change among Machair grasslands influences community assembly processes? (Chapter 4).

- Is climate important in governing processes of species temporal turnover within the Machair grasslands, and how do different measurable components of climate influence directional change in species richness differences and species replacement components of turnover? (Chapter 5).

- How important are patterns in spatial turnover in capturing patterns in temporal turnover? (Chapter 5).

6.1 What is the relative importance of land use management and climate as drivers of spatial vegetation patterns among Scotland's soft coasts?

Management and climate were shown to explain significantly the spatial vegetation patterns among Scotland's soft coast habitats (Chapter 2). For both the full national-scale data and that of a smaller subset representative solely of Machair sites, environmental descriptors of land use management were found to capture more spatial variation than climate, suggesting that land use management predominates over climate in governing spatial vegetation patterns of Scotland's soft coasts. Important management determinants were those that measure vegetation structure, proxies for several determinants of vegetation composition such as grazing intensity and disturbance. This suggests a significant spatial pattern in Scottish coastal vegetation as a result of different management regimes, reaffirming the significance of disturbance in governing plant species compositional assemblages of coastal grasslands (Oosterveld 1985; Aptroot et al. 2007; Plassmann et al. 2010). Although, second to management in terms of variation captured, all measured climatic descriptors were identified as significantly capturing spatial variation. Among the national-scale data, potential evapo-transpiration and oceanicity, indicative of wetter climatic regimes in the west were identified as out-performing other climatic measures. This suggests a significant difference in vegetation composition along a longitudinal gradient across Scotland, explained in part by variation in climate. On the other hand, a latitudinal gradient was identified among those sites inclusive of Machair habitat, where humidity and growing degree days best captured spatial vegetation patterns. This suggests the warmer drier climes of more southerly site such as Islay, Coll and Tiree of the Inner Hebrides have, statistically, very different vegetation assemblages compared to northern Machair sites, for example; Lewis, the North Coast, Orkney and Shetland.

6.2 How are land use and climatic determinants of Scotland's soft coast spatially scaled, and what can this tell us about the community assembly processes that operate to govern the vegetation assemblages of these communities?

It was clear that measured and unmeasured spatially dependent determinants of Scotland's soft coast vegetation operate predominantly at broad spatial scales (Chapter 2). Climatic determinants were shown to contribute a large proportion of the spatial variation captured at the broad scale, for both national and Machair datasets, and were probably representative of the latitudinal and longitudinal climatic gradients. Similarly, land use management also displayed a degree of broad-scale spatial structuring, much of which was shared also with climate. A clear correlation between variables measuring vegetation structure and broad-scale spatial variables for both the national extent and Machair data, suggest differences in the vegetation composition between these sites furthest apart. Among the national data, this is discussed in terms of Machair and non-Machair management along a longitudinal gradient. This probably represents a difference in vegetation structure between the east and west coasts of Scotland, as the presence and significant cover of shrubs and tree species were only reported for sites on the east coast. In terms of coastal dune conservation, this raises concerns of over-stabilisation of Scotland's coastal grasslands on the eastern seaboard. For the Machair data, it suggests different land use management regimes between islands, indicating significant differences between those furthest apart. Results may in part be explained between regions traditionally crofted and subsidised specifically to maintain their herb-rich Machair grasslands through the ESA government scheme (e.g. Barra, Benbecula and North and South), and those regions which fell outside the ESA protection altogether (e.g. Harris, Lewis, the North Coast and Orkney).

Results suggest that processes of environmental filtering, principally through climate, and to some extent management, operate at relatively broad spatial scales in governing the vegetation composition of Scotland's soft coast habitats. However, a significant independent fraction of meso- and fine scale spatial variables allude to important, spatially-dependent yet unmeasured environmental determinants, potentially representing soil chemistry, which would infer further environmental filtering at less-broad scales, and or stochastic neutral processes such as seed dispersal operating at relatively fine spatial scales.

Furthermore, given the relative importance of land use management variables, partitioning the spatial component found management to be poorly represented in comparison to climatic determinants. It was concluded that the spatial resolution of the Scottish Coastal Survey is too broad to detect spatially dependent land use determinants operating at a scale of less than 1.5km. This is perhaps not an issue for most semi-natural grassland studies, except for Machair, where owing to successional, soil chemical and disturbance gradients, including multiple land users, the Machairs display exceptionally high heterogeneity over relatively small distances. It appears then that the influence of environmental filtering at relatively fine scales may have been underestimated. Furthermore biotic processes such as competition and facilitation also require a fine spatial resolution dataset in order to be detected. Results do, however, suggest that different community assembly drivers are not mutually exclusive, and in fact operate on a scale-dependent basis.

6.3 What are the major shifts in plant species assemblages of the Machair system and Machair grassland over 30 years of change, and can changes in land use or climate be linked to changes in vegetation?

Analyses of spatial-temporal data, based on two sample periods (1976 and 2010) identified significant national and regional-scale shifts in species composition for both Scottish Machair systems and their associated grasslands (Chapter 3). Several regions displayed increased species richness over the 30-year time period, including significant gains in those species indicative of good quality Machair grasslands. This study reports a trend between regions demonstrating increased biodiversity and favourable plant species for Machair conservation with regions that received agri-environment funding through designation as an Environmental Sensitive Area (ESA). These schemes provided crofters and farmers with financial incentives to manage their land in an environmentally beneficial manner, typically ensuring that low-intensity rotational arable agriculture and winter grazing was maintained, and preventing intensification, use of inorganic fertilisers and the erecting of fencing to permit summer grazing of cattle. Results suggest that there were benefits of targeted, incentivized management for biodiversity conservation of the Machairs. This is of upmost importance for successful future conservation, as increasing pressures of socio-economic change, continue to discourage forms of traditional management that struggle to be socially and economically viable (Angus and Hansom 2004).

The patterns displayed among ESA-designated areas and increased biodiversity were however, not consistent across all ESA surveyed sites. North Uist, Benbecula and Shetland showed evidence of biodiversity loss, and significant falls in species indicative of good quality Machair within the Machair grassland. Shifts in plant functional strategies for these regions could be linked to declines (N.Uist and Benbecula) and increases (Shetland) in grazing management, indicating current disturbance regimes to be unfavorable for maintaining the biodiversity of the Machair. Similarly declines in active management are almost certainly responsible for reducing the biodiversity value of the Machair on Harris, Lewis and the Monachs with some evidence raising concerns of biotic homogenization. Results relate to the intermediate disturbance hypothesis of Connell (1978), in which moderate disturbance regimes give rise to greatest number of plant species. This has particular importance for the Machairs, which are not a natural habitat, but have developed in tandem with human settlers over centuries. The floristic diversity of the Machair grasslands is dependent on some form of moderate disturbance, typically through active land use for cultivation and livestock (Angus and Dargie 2002; Angus 2009). Therefore this study raises particular concerns for North Uist and Benbecula, regions considered to support some of the best examples of Hebridean Machair (Angus 1996).

However, regions displaying biodiversity gains should also be monitored carefully. Patterns displayed among plant functional strategies and Ellenberg indicators for Shetland (a region showing significant biodiversity loss, particularly among Machair specialists) were mirrored (although to a lesser extent) by regions displaying biodiversity gains (Colonsay, Islay, and South Uist). Significant falls in the stress tolerator (CSR-S) component and significant gains in species representative of high Ellenberg Nitrogen values, substantiate other works raising concerns over the use of inorganic fertilisers (Nolan et al. 1998; Pakeman et al. 2011). In the relatively short-term it would seem inorganic fertiliser application is yet to impact on the taxonomic diversity of the Machairs. However in the long-term, concerns have been raised over the soil-stabilising qualities of this shift away from applying organic alternatives, traditionally seaweed. With forecasted climate scenarios of deeper depressions for the Outer Hebrides, resulting in higher winds and prevalence of storms (Angus and Hansom 2004), the Machairs will be subject to increasing sand-blow and natural erosive forces. This study highlights a significant increase among both the Machair system and its grasslands in the prevalence of *Leymus arenarius*, a species extremely tolerant to sand burial, raising concern over the current stability of

Scottish Machairs and their resilience and ability to maintain its biodiversity among future climate scenarios.

6.4 Can temporal patterns of plant functional traits help to confirm observed and reported shifts away from traditional land use management among the Machair grasslands?

Classical biodiversity measures, such as species richness as assessed in Chapter 3, rely on several assumptions surrounding the relative equality of species and individuals (Peet 1974; Magurran 2004). It is well known however, that species maintain very different functional characteristics, allowing them to perform differently in differing environments (Grime et al. 2007), hence invalidating the assumption of species being equal. Nevertheless, to understand patterns of biodiversity in space and time, ecologists are required to quantify them (Purvis and Hector 2000), and as a result, species richness, and several richness indices have become standard biodiversity monitoring units. However, biodiversity is increasingly measured in terms of genes, phenotypes and functional traits. The work in Chapter 4 focuses on the latter (i.e. plant functional traits) and is a natural progression and extension to the analyses presented in Chapter 3, providing a framework not solely to monitor biodiversity change but also to investigate how drivers of change may be influencing community assembly processes (Mouchet et al. 2010).

The analyses clearly demonstrate a significant change in the functional composition of the Machair grassland, identifying several Machair regions to be more disturbed (North Coast, Sanday and Tiree) or less disturbed (Barra, Monachs, N.Uist and S.Uist) through comparison of vegetative trait values: vegetation height (VH), leaf dry matter content (LDMC) and specific leaf area (SLA). The biodiversity value of Machair grasslands appears to display a quadratic response to disturbance (Connell 1978), i.e. diversity is greatest at intermediate levels of disturbance. However, it is difficult to interpret whether significant gains or declines along disturbance gradients augment or detract from the conservation value. However, interpretation of results obtained by classical biodiversity measures used in Chapter 3 suggests increased disturbance among the North Coast and Sanday may be responsible for the significant negative impact on taxonomic biodiversity (Scenario B, Fig. 6.1), particularly Machair specialists (Sanday), while similarly responsible for taxonomic biodiversity gains for Tiree (Scenario A, Fig. 6.1). Further, declines in disturbance appear to negatively affect the biodiversity of Machair grassland for the Monachs and N.Uist (Scenario D, Fig. 6.1.), whilst showing a positive affect for Barra and S.Uist (Scenario C, Fig. 6.1).

Analyses of functional traits also found strong evidence of change in the regenerative traits of Machair grassland plants, identifying significant gains in wind-pollinated species with significant falls in insect pollinated plants. Results suggest an overwhelming decline in agricultural weeds, probably as a result of shifts away from rotational arable agriculture. Where the use of artificial fertiliser has increased, as evidenced in Chapter 3, traditional practices of resting the land to recoup nutrients can become superfluous. This not only significantly affects the functional and taxonomic diversity of the Machair grasslands but also the many species that ultimately depend on these floras particularly nationally rare species of insects (Goulson et al. 2005; Redpath et al. 2010), and birds (Fuller et al. 1986; Angus 2001). The gain in wind-pollinated species is likely to be a result of an increase in the abundance of grasses, which may have followed from the reduced grazing intensity reported for many Machair regions (Pakeman et al. 2011), as taller, dominant grasses predominate.

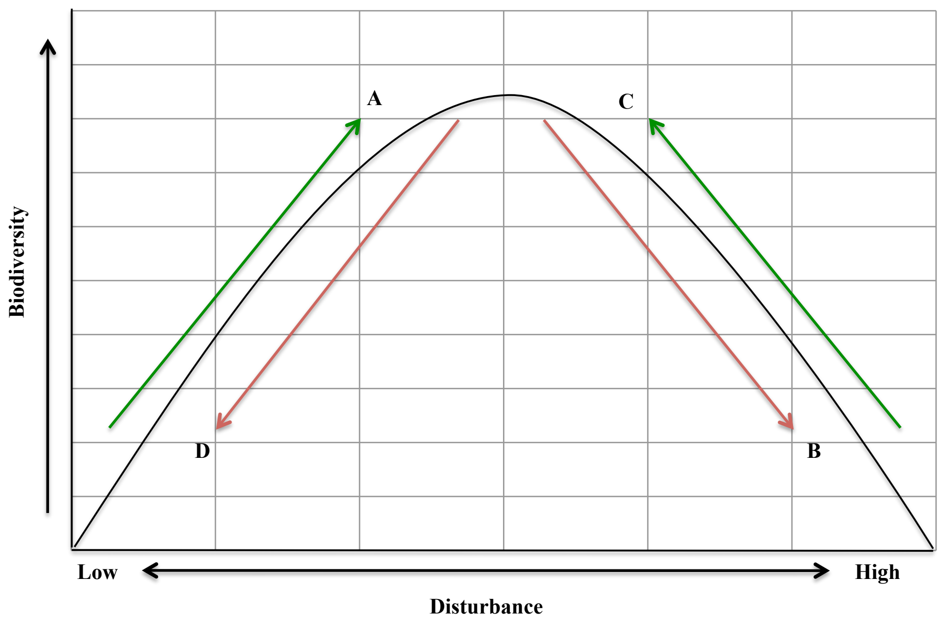


Fig. 6.1 Schematic diagram representing different scenarios of biodiversity change with shifts along a disturbance gradient for Machair grasslands. (A) Increased disturbance with resulting biodiversity gain; (B) Increased disturbance with resulting biodiversity loss; (C) Decreased disturbance with resulting biodiversity gain; (D) Decreased disturbance with resulting biodiversity loss.

6.5 Can functional trait diversity; measured using Richness, Divergence, Evenness and Dispersion indices help to identify how land use change among Machair grasslands influences community assembly processes?

Mouchet et al. (2010) provided a framework for interpreting Functional Diversity (FD) indices against randomly simulated values, which would be expected through chance. They suggest that lower than expected values of Functional Richness (FRic), which measures the volumes of functional trait space of a community, and Functional Evenness (FEve), which measures the regularity of the distribution in abundance within this volume, indicate habitat filtering, caused by some process of the abiotic environment acting to constrain a given plant community. Further, greater than expected values of Functional Divergence, which represent the spread of species within the trait space, are suggested to indicate niche differentiation or limiting similarity (MacArthur and Levins 1967). Functional dispersion (FDis) is thought to behave similarly to FRic (Laliberté and Legendre 2010), but is a weighted measure, so it is less sensitive to rare, functionally-unusual species.

Results presented in Chapter 4 provide evidence of both niche filtering and limiting niche similarity, providing support that these processes are not mutually exclusive, but act simultaneously in governing the vegetation of Scottish Machair grasslands. Investigation of temporal change in FRic and FDis from expectation identified several regions to be statistically more constrained today, compared to 1976, displaying significant declines in these functional diversity components. FRic and FDis were shown to be correlated with disturbance gradients, declining with increased disturbance, so that functional trait space becomes smaller and species become more functionally similar (Laiberté et al. 2010), suggesting that increased land use intensity results in greater prevalence of niche filters, supporting the findings of Pakeman (2011). However, when put into context for Machair conservation, most areas identified as displaying significantly reduced functional dispersion (Barra, Islay, South Uist and Tiree) are regions reported in Chapter 3 to have increase in biodiversity, significantly so for Machair specialist and fallow species. Perhaps then, species that are considered important for Machair conservation do not differ greatly in their functional characteristics. Since functionally similar communities are considered to be more vulnerable to land use change (Laliberté et al. 2010), this is perhaps further evidence as to why Machair biodiversity is so sensitive to change in land use practices away from low-intensity rotational agriculture and livestock grazing.

This study shows little evidence that limiting similarity is becoming more prevalent at a national-scale. However, on a regional scale, Colonsay displayed the only reported significant increase. Typically these processes are governed by biotic interactions such as competition, which have been found to intensify with reduced disturbance through grazing (Pakeman 2004). However, for Colonsay the results may well reflect the large increase in species richness in the Machair grassland system reported in Chapter 3.

6.6 Is climate important in governing processes of species temporal turnover within the Machair grasslands, and how do different measurable components of climate influence directional change in species richness differences and species replacement components of turnover?

Climate was shown to influence significantly the temporal turnover patterns in Machair grassland species (Chapter 5). Although total variation captured by climatic variables was low (ca. 5-7%), models with climatic covariates were found to outperform significantly, those models where climatic information was excluded. This study provides further evidence that the species composition of Machair grasslands is governed by environmental filters at a relatively broad scale through climatic variation, supporting results reported in Chapter 2. Furthermore, it empirically links compositional change in Machair plant communities to changes in the climate since the original survey in 1976. This raises further conservation concern over maintaining the biodiversity values of Machair habitats, as climate change, coupled with changes in land use management (Pakeman et al. 2011) may accelerate plant compositional change, potentially impacting upon Machair taxonomic (Chapter 3), and functional diversity (Chapter 4).

A widely-used index of turnover (β-diversity) is the Sørensen index (Sørensen 1948), which captures β-diversity in all its components, that is species richness differences through recruitment and loss, and, compositional change through species replacement. However, this study demonstrates the utility of a multi-index approach to measuring β-diversity, specifically in the use of indices that dissect β-diversity into its individual measurable components, i.e. richness and replacement. This approach allows the user to investigate how different processes (here climatic) impact on spatial or temporal patterns of change, as a result of either: species gain or species loss (i.e. biodiversity change), and species replacement (i.e. compositional change). Further, it allows insight into whether drivers of change influence these components of turnover equally or differently; patterns that cannot possibly be identified through use of an index that captures both components simultaneously. Using this approach, this work clearly demonstrates richness and replacement components can show a very different response to some component variables of climate. For examples, where the long-term trends in minimum temperature were steepest (i.e. Lewis and Harris), species replacement increased and richness differences declined. In other words a steeper change towards warmer climes influenced compositional change, whilst it dampened the change in overall diversity. In fact, from all measured component variables of climate, only one, long-term change in water balance (drought), displayed a consistent pattern with all metrics of turnover, showing that increased drought significantly promotes temporal turnover for both the richness and replacement components and also, species relative abundance change, measured using the Bray-Curtis abundance index (Bray and Curtis 1957). The latter was included in the analyses with the expectation that a non-binomial index, which extends beyond presence and absence data to include compositional assemblage of species, should capture the greatest proportion of temporal variation. However, this was not the case, as results reveal little difference between the binomial and abundance indices in capturing variation explained by climate. Further when spatial turnover was included in the models, Sørensen's index was found to perform best when modelling both climate and spatial covariates.

6.7 How important is spatial turnover in capturing patterns in temporal turnover?

Inclusion of spatial turnover as a model covariate was shown to significantly improve turnover models, capturing more variation in temporal turnover than models including only climatic covariates (Chapter 5). This outcome is perhaps not unsurprising. Machair grasslands are part of a highly heterogeneous landscape, owing to many spatially-dependent factors such as soil chemistry (Pakeman et al. 2008), multiple land-ownership and exposure at relatively local- and meso-scales. Spatial turnover measures are likely to capture some of the variation owing to these external environmental determinants, thus improving variation explained by models with spatial-turnover covariates. Therefore understanding processes that govern spatial turnover, as investigated in Chapter 2, should similarly improve understanding of the patterns and processes that drive temporal turnover. This finding of a positive spatial-temporal-turnover relationship is congruent with earlier studies (Ptacnik et al. 2008; Ptacnik et al. 2010; Stegen et al. 2012), and supports the notion that patterns in spatial and temporal turnover are inextricably linked (Alder et al. 2005; White et al. 2006). However, this study shows that indices that measure individual components of turnover, i.e. richness gradients and species replacement perform very differently in capturing spatial variation. Results suggest spatial turnover exerts little influence on richness gradients in comparison with species replacement. Understanding the reasons for why this may be the case for plant communities of Machair grasslands is not straightforward and certainly warrants further investigation.

6.8 Limitations

This thesis examines spatial-temporal data of almost an entire national resource. As with most large scale studies, a certain amount of error must be expected. This is particularly true for re-surveys of historic data, from non-permanent vegetation plots. Error becomes further compounded with, for example: shifts in the onset of flowering with temporal changes in seasons, and, multiple survey teams and different recorders of the re-survey. Nevertheless, the work presented in this thesis demonstrates, despite these unavoidable errors, vegetation re-surveys of historic, non-permanent vegetation plots, can provide valuable temporal data. Providing due care is followed to ensure the accuracy of sample locations and original survey methodology is honoured, re-surveys as conducted here, provide powerful datasets, where biological variation in space and time can be successfully explained by environmental parameters, providing understanding of the processes that govern vegetation communities.

Sampling error, particularly relocation error, is problematic when examining temporal turnover, as sampling the wrong area increases the likelihood of recording temporal turnover, where in-fact the vegetation community may not have changed. Because it's inevitable that relocation error inflates temporal turnover, even the slightest re-location inaccuracy is possible to inflate levels of turnover as calculated in Chapter 5. However, for the statistical models applied in Chapter 5, this should be relatively unimportant because the inflation of turnover should simply make the intercept larger and the proportion of unexplained variance of the model larger, thus having little affect on the power of the model to capture variation in the data.

Throughout the research presented in this thesis, many procedures of statistical analysis have been applied, few of which are not without alternatives approaches, and as is often the case, schools in favour of one method over another and *vice versa*. In Chapter 2, analyses involved the use of Principal Coordinates of Neighbour Matrices (PCNM) to investigate the multi-scale spatial structure of environmental determinants and a stepwise selection procedure as a model parameter selection method.

PCNM analysis is useful for modelling multi-scale spatial structures (Borcard & Legendre, 2002), and is a great advance upon earlier studies that used trend surface polynomial regression (Gilbert & Lechowicz 2004). However, truly fine-scale biotic processes such as species territoriality, or competition, important biotic processes that govern vegetation assemblages, exhibit much finer spatial scales than the resolution of the Scottish coastal survey data. To detect such fine scale processes, not only is a study design with a fine spatial grain and spatial lag required, but also a different spatial analyses tool, as biotic determinants most likely correspond to negative eigenvalues (negative spatial autocorrelation), eigenvalues that in the PCNM analysis are removed. Here, the method of choice would be Moran's Eigenvector Maps (MEM). Similar mathematically to PCNM, MEM retains eigenvectors with negative eigenvalues, explaining 100% of a 'n' cantered matrix (Dray et al. 2006).

Ecological data often consists of many explanatory environmental variables to try to better understand how and why species and communities are structured (Blanchet et al. 2008). The purpose when analysing the data is to establish a suite of variable that constitutes towards a best approximating model, or rather a parsimonious model, from which to develop statistical inferences (Burnham and Anderson 2002). In ecology, a general rule that models with fewer variables also contain fewer nuisance variables and greater predictive power (Gauch 1993) tends to hold true (Ginzburg and Jensen 2004), and a widely recognised procedure to achieve model parsimony is termed 'stepwise forward selection'. However, biases and shortcomings of stepwise selection are also well established (Johnson et al. 2004; Stephens et al. 2005), of which the principal concern is in the over-estimation of the amount of explained variance, and highly inflated Type I error (i.e. falsely rejecting the null hypothesis). These shortcomings were circumvented in the model selection procedure in Chapter 2, through use of an improved forward selection procedure (*see* Blanchet et al. 2008). However, despite this newly improved method, the unpredictable nature of forward selection methodologies continues to be scrutinised, and it is argued that better approaches do exists (Anderson et al. 2000). One such approach rests on Akaike's information criteria (AIC), which provides a simple, effective and objective means for selection of an estimated *best approximating model* (Burnham and Anderson 2002). This form of model selection and model inference is known as the information-theoretic approach, discussed in detail in Burnham and Anderson (2002), and is applied in the analysis of temporal turnover of the Machair grassland in Chapter 5.

However, not least in terms of scrutiny received, is the method of Principal Component Analysis and its constrained counterpart, Redundancy Analysis (RDA), when applied to non-linear or unimodal data tables. In nature, most species only occupy part of an environmental gradient, whereby beyond the end of a species response curve, a replacement is made by another species along that gradient. When captured in large ecological datasets, species replacement generates many zeros in the species data table; a feature of all Gaussian species response curves termed the “zero truncation problem” (Kent 2012). Such unimodal distribution of data when applied to linear models of PCA and RDA are known to result in a curvilinear representation of community gradients in ordination space, a phenomenon termed “horseshoe effect”, whereby the Euclidean distance between two sites, that share zero species, is found to be smaller than distances between sites sharing two or more species (Legendre and Gallagher 2001). To overcome this distortion issue, linear ordination methods in this thesis (Chapter 2, Chapter 3, Chapter 4) were applied to ecological data, post Hellinger transformation proposed by Legendre and Gallagher (2001). The transformation involves standardising the species data matrix by sample total and taking the square root of each element in the matrix. Analysing the resultant matrix using Euclidean distance methods thus results in a matrix of Hellinger distances (Kent 2012). However, despite many advocates of this procedure, recent results generated from simulated species assemblages with varying beta diversities, identified PCA to perform poorly despite the use of the Hellinger transformation (Mitchin and Rennie 2010).

Those opposed to using the Hellinger transformation for PCA and RDA would likely advocate the use of an alternative method, such as, non-metric multidimensional scaling (NMDS). Increasingly used over the past 20 years, its advantage over Euclidean based methods is that it does not assume a linear relationship between species. Furthermore, ranked distance measures that linearise the relationship between distances measured in species space and distances measured in environmental space overcomes the ‘zero-truncation’ problem (Kent 2012). The analysis presented in Chapter 3 relies heavily on the Hellinger transformation and Euclidean ordination methods. It would therefore be interesting to see if similar inferences are derived from substituting this approach with NMDS. In the first instance, complication would arise in terms of computational complexity when applied to the Machair dataset, given the number of survey plots, however this may be overcome by analysing data a regional levels or alternatively an area scale which distinguishes those regions once designated as environmentally sensitive areas (ESA, *See Chapter 3*). This would also provide an empirical test of PCA *vs* NMDS methods on large-scale unimodal data where beta diversity is high, a feature argued to exacerbate the ‘horse-shoe effect’ (Mitchin and Rennie 2010).

6.9 Further Research

This thesis contributes valuable new evidence regarding the ecological changes that have occurred across one of Britain and Europe’s most biodiverse cultural landscapes. It identifies spatial and temporal shifts among different facets of biodiversity, i.e. species and functional diversity at national and regional scales. It furthermore highlights the significance of land use and climate as drivers of these changes. Nevertheless, there are several areas of this thesis where further research could advance understanding of how environmental drivers impact upon the biodiversity of this internationally important habitat whilst simultaneously demonstrating the application of new methodological and statistical approaches for exploring spatial and temporal biodiversity patterns.

Chapter 2 investigates the relative importance of land use and climatic drivers in governing spatial diversity patterns. Further it uses principal component of neighbour matrices to assess the spatial scales at which these driver appear to operate. A natural progression of this work would be to substitute the species data matrices with functional trait data, to investigate whether the effects of land use and climate operate at similar functional diversity compared to taxonomic diversity, and whether using functional trait data as opposed to species identity, reveals the measured environmental determinants to explain better the species functional variation, compared to species compositional variation. Similarly applying functional trait data to the methods used in Chapter 5 would provide further insight into how climate might influence the functional composition of the Machairs in time, i.e. functional turnover. This approach should provide greater understanding of how changing climate might affect ecosystem processes, reduce or increase ecosystem resilience and impact on community assembly processes. Equally, covariables that best capture land use management could be applied instead of climatic measures. This approach could be used to further support many of the findings presented in this thesis, that land use change is significantly affecting the compositional and functional diversity of the Machairs, identifying empirically, measures linked to specific land use changes, that have the greatest impact on the biodiversity value of the Machairs.

Analyses of Chapter 2 identified that the spatial grain of the Scottish Coastal Survey data is too broad to permit identification of much of the local scale spatially-dependent drivers, particularly important land use variables. Given the extremely heterogeneous nature of Machair grasslands over relatively short distances (typically a few hectares), a survey at a much finer spatial resolution, over a few carefully selected sites would allow for much of this finer-scaled spatial heterogeneity to be captured. This would ensure to identify how land use and other local-scale factors (e.g. soil chemistry) operate, providing more detailed knowledge for the successful implementation of conservation management.

The work presented here demonstrates that community assembly processes operate simultaneously, and at varying hierarchical scales. It is clear that environmental heterogeneity operates to influence the vegetation of the Machairs at both relatively broad and smaller spatial scales. However, the role of limiting similarity (biotic processes) is less well defined. Vegetation data collected at an extremely fine-scale ($< 1m^2$) would allow identification of biotic interactions, investigating their relative importance in governing spatial vegetation patterns of the Machair. The approach used in Chapter 2 could be followed to investigate the spatial dependence of biotic interactions. However, the PCNM methodology would be best substituted for Morans Eigenvector Mapping (MEM) discussed above, which captures negative as well as positive spatial eigenvectors (Dray et al. 2006), and is a far better approach for investigating truly fine scale interactions.

Further, repeat surveys of such fine resolution data would permit the investigation of how biotic interactions influence temporal turnover patterns. This could be addressed in terms of both taxonomic turnover and functional turnover using similar approaches to those applied in Chapter 5. An extension to this may be to investigate a relatively new approach to dissecting beta diversity, to include what has been termed the “nestedness” component (Baselga 2010). Nestedness of species assemblages occurs when an assemblages of species of one sites is a subset of a neighbouring site, either in space or time. The processes behind “nestedness” results only in species loss and are thought to be antithetic to those processes responsible for species replacement i.e. species turnover (Baselga 2010; Podani and Schmera 2011). Therefore, disentangling the two processes, which theoretically represent contrasting ecological phenomena captured within beta diversity, should provide a better understanding into the processes that govern vegetation communities.

Collecting further data on the vegetation composition of the Machairs at such a fine resolution should provide an extremely unique spatial-temporal national dataset, with a nested hierarchal spatial resolution, allowing the investigation of biotic and abiotic drivers of different facets of biodiversity change for a globally-rare semi-natural grassland habitat.

Finally, the methods and approaches used to investigate spatial and temporal facets of biodiversity in this thesis can be similarly applied to vegetation datasets beyond that of the Machair. It may be of interest to extend beyond a national-scale study of low intensity, cultural grassland to include similar habitats confined to other geographical areas of Europe. For example, alvar grasslands, thin-soil calcareous grasslands on Ordovician or Silurian limestone bedrock (Partel 1999) is another semi-natural grassland of high nature conservation priority in Europe. Found predominantly in Sweden and Estonia (but also some in North America), alvar grasslands, like Machair, have developed in close association with human land use. A comparative analysis, particularly of fine-resolution data, may be interesting to investigate whether biotic interactions, assembly processes and functional trait turnover behaves similarly under similar disturbances for both the Machair and alvar grasslands.

6.10 Conclusion

This thesis makes a contribution to knowledge of how land use and climate affects spatial and temporal patterns in plant species biodiversity of Scotland’s soft coast habitats, with a specific focus on Machair. From a Machair conservation perspective, progress has been made towards a better understanding of the role of differing environmental determinants and community assembly processes, how they operate to govern vegetation composition and the relative spatial scale at which these determinants operate, furthering knowledge of how pressures of land use and environmental change impact biodiversity. In terms of investigating spatial and temporal biodiversity patterns, this thesis further demonstrates the utility of different analytical methods, such as multi-scale spatial predictors, functional diversity indices, and a multi-turnover index approach, for disentangling patterns and processes that shape biodiversity, ultimately providing greater insight into how vegetation communities are likely to respond to future environmental scenarios.

REFERENCES

Alder, P.B., White, E.P., Lauenroth, W.K., Kaufman, D.M., Rassweiler, A. and Rusak, J.A. 2005. Evidence for a general species-time-area relationship. Ecology 86, 2032-2039.

Anderson, D.R., Burnham, K.P. and White, G.C. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64, 311-316.

Angus, S. 1996. Natural heritage conservation in the Southern Outer Hebrides. In: Gilbertson, D., Kent, M. & Grattan, J. (eds.) The Outer Hebrides: the last 14,000 years, pp. 227- 250. Sheffield Academic Press, Sheffield.

Angus, S. 2001. The Outer Hebrides: moor and machair. The White Horse Press, Cambridge/Isle of Harris, UK.

Angus, S. and Dargie, T. 2002. The UK Machair habitat action plan: progress and problems. Botanical Journal of Scotland 54, 63-74.

Angus, S. and Hansom, J.D. 2004. Tir a' Mhachair, Tir nan Loch? Climate change scenarios for Scottish Machair Systems: A wet future? Proceedings Vol.2. Littoral 2004. Delivering sustainable coast: connecting science and policy. 565-569.

Angus, S. 2009. Dé tha cearr air a'mhachaire? Biodiversity issues for Scottish Machair: an initial appraisal. The Glasgow Naturalist 25, Supplement. Machair Conservation: Successes and Challenges, 53-62.

Angus, S., Hansom, J. and Rennie, A. 2011. Habitat change on Scotland's coasts. Marrs, S.J., Foster, S., Hendrie, C., Mackey, E.C. and Thompson, D.B.A. (eds) The Changing Nature of Scotland,183-198. TSO, Edinburgh.

Anon. 2008. UK biodiversity action plan priority habitat descriptions: Machair. JNCC. Peterborough.

Aptroot, A., van Dobben, H.F., Slim, P.A., Olff, H. 2007. The role of cattle in maintaining plant species diversity in wet dune valleys. Biodiversity Conservation 16, 1541-1550.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134-143.

Blanchet, F.G., Legendre, P., Borcard, D. 2008. Forward selection of explanatory variables. Ecology 89, 2623-2632.

Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153, 51-68.

Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27, 325-349.

Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference. Springer, New York.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Dargie, T.C.D. 2000. Sand dune vegetation survey of Scotland: National Report. Scottish National Heritage, Perth.

Dray, S., Legendre, P. and Peres-Neto, R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196, 483-493.

Fuller, R.J., Reed, T.M., Buxton, N.E., Webb, A., Williams, T.D. and Pienkowski, M.W. 1986. Populations of breeding waders (Charadrii) and their habitats on the crofting lands of the Outer Hebrides. Biological Conservation 37, 333-361.

Gauch, H.G. 1993. Prediction, parsimony and noise. American Scientist 81, 468-478.

Gilbert, B. and Lechowicz, M.J. 2004. Neutrality, niches, and dispersal in temperate forest understory. Proceedings of the National Academy of Sciences 101, 7651-7656.

Ginzburg, L.R. and Jensen, C.X.J. 2004. Rules of thumb for judging ecological theories. Trends in Ecology and Evolution 19, 121-126.

Grime, P., Hodgson, J.G. and Hunt, R. 2007. Comparative plant ecology: a functional approach to common British species. Second Edition. London, Unwin Hyman.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.E. and Knight, M.E. 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1–8.

Johnson, C.J., Seip, D.R. and Boyce, M.S. 2004. A quantitative approach to conservation planning: using resource selction functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41, 238-251.

Kent, M. 2012. Vegetation description and data analysis: a practical approach. 2nd ed. John Wiley & Sons Ltd. Oxford

Laliberté, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91, 299–305.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P. et al. 2010. Land use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters 13, 76-86.

Legendre, P. and Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

MacArthur, R. and Levins. R. 1967. Limiting similarity convergence and divergence of coexisting species. American Naturalist 101, 377.

Magurran, A.E. 2004. Measuring biological diversity. Oxford: Blackwell Publishing

Mitchin, P.R. and Rennie, L.D. 2010. Does the Hellinger transformation make PCA a viable method for community ordination? Paper presented at the 95th Ecological Society of America Anuual Meeting, August 2010. Available at http://eco.conflex.com/eco/2010/techprogram/P24489.HTM [accessed 01 August 2012].

Mouchet, M.A., Villéger, S., Mason, N.W.H. and Mouillot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24, 867-876.

Nolan, A.J., Henderson, D.J., Bell, S.J. and Gauld, J.H. 1998. The Environmentally Sensitive Areas designated in Scotland: The machair of the Uists and Benbecula, Barra and Vatersay ESA monitoring report. Macaulay Land Use Research Institute, Scotland.

Oosterveld, P. 1985. Grazing in dune areas: the objectives of nature conservation and the aims of research for nature conservation management. In: Doody, J.P. Sand dunes and their management. pp. 187-203. Nature Conservancy Council, Peterborough, UK.

Pakeman, R.J. 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. Journal of Ecology 92, 93-905.

Pakeman, R.J. 2011 Functional diversity indices reveal the impacts of land use intensification on plant community assembly. Journal of Ecology 99, 1143-1151.

Pakeman, R.J., Reid, C.L., Lennon, J.J. and Kent, M. 2008. Possible interactions between environmental factors in determining species optima. Journal of Vegetation Science 19, 201-208.

Pakeman, R.J., Huband, S., Kriel, A. and Lewis, R.J. 2011. Changes in the management of Scottish Machair communities and associated habitats from the 1970s to the present. Scottish Geographical Journal 127, 267-287.

Partel, M., Kalamees, R., Zobel, M. and Rosén, E. 1999. Alvar grasslands in Estonia: variation in species composition and community structure. Journal of Vegetation Science 10, 561–570.

Peet, R.K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5, 285-307.

Plassmann, K., Laurence, M., Jones, M., Jones, G.E. 2010. Effects of long-term grazing management on sand dune vegetation of high conservation interest. Applied Vegetation Science 13, 100-112.

Podani, J. and Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence/absence data. Oikos 120, 1625-1638.

Ptacnik, R., Solimini, A.G., Anderson, T., Tamminen, T., Brettum, p., Lepisto, L., Willén, E. and Rekolainen, S. 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. Proceedings of the National Academy of Sciences 105, 5134-5138.

Ptacnik, R., Anderson, T., Brettum, P., Lepisto, L. and Willén, E. 2010. Regional species pools control community saturation in lake phytoplankton. Proceedings of the Royal Society B: Biological Sciences 277, 3755-3764.

Purvis, A. and Hector, A. 2000. Getting the measure of biodiversity. Nature 405, 212–219.

Redpath, N., Osgathorpe, L.M., Park, K., Goulson, D. 2010. Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland. Biological Conservation 143, 492-500.

Sørensen, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Dannish commons. Kongelige Danske Videnskaernes Selskabs Biologiske Skrifter 5, 1-34.

Stegen, J.C., Freestone, A.L., Crist, T.O., Anderson, M.J., Chase, J.M. et al. 2012. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. Global Ecology and Biogeography, online.

Stephens, P.A., Buskirk, S.W., Hayward, G.D. and Martinez del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology 42, 4-12.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., et al. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14, 1125-1140.

White, E.P., Alder, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., et al. 2006. A comparison of the species-time relationship across ecosystems and taxonomic groups. Oikos 112, 185-195.