DOCTOR OF PHILOSOPHY

Biodiversity, ecosystem function and ecosystem service provision in saltmarsh and sand dune grasslands

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BIODIVERSITY, ECOSYSTEM FUNCTION AND ECOSYSTEM SERVICE PROVISION IN SALTMARSH AND SAND DUNE GRASSLANDS

A thesis submitted to Bangor University
by

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Summary

Coastal grasslands, such as salt marshes and sand dunes, provide many important ecosystem services including 'supporting services' (soil formation, primary productivity and nutrient cycling), 'provisioning services' (fresh water supply, food and fibre products, bio-chemical or genetic resources), 'regulating services' (equable climate, pollution control, flood prevention, invertebrate pollination and pest regulation) and 'cultural services' (recreation, education and aesthetic appreciation). Historically, salt marsh and sand dune grasslands were commonly used as agricultural livestock grazing land. Currently, some of these coastal grasslands are 'conservation grazed' (i.e. extensively grazed to maximise plant diversity and to provide a suitable habitat for over-wintering bird species), others have been 'abandoned' (i.e. large herbivores removed) due to the removal of agricultural subsidies or remain historically 'un-grazed'. Grazing management of coastal grasslands influences biological and physical habitat characteristics, ecosystem function, biodiversity and ecosystem service delivery. Understanding the impact of grazing is therefore vital to enable future robust management recommendations. Biodiversity is often used as an indicator of ecosystem health and ecosystem service provision with conservation priorities allocated accordingly. It is therefore essential to critically assess just how important biodiversity is to the provision of ecosystem services within a wide range of habitats. The review chapter draws together evidence for this argument from salt marsh and sand dune habitats with the conclusion that functional diversity and composition are more important than biodiversity *per se* (Chapter 2). The experimental chapters of this thesis deal with the impact of grazing upon temperate salt marsh and sand dune grassland biodiversity and ecosystem service provision. 'Grazed' (cattle grazed < 8 cm) and historically 'un-grazed' upper salt marsh plots were compared. 'Fully grazed' (ponies 0.2 ha^{-1}, cattle 0.05 ha^{-1} and rabbits 45 ha^{-1}), 'rabbit grazed' and 'un-grazed' (for 8 years) fixed sand dune grassland plots were also evaluated. Firstly, how grazing management affected ecosystem service provision of sand dune grassland was examined, by measuring a wide range of biophysical variables as proxies for ecosystem services (Chapter 3). 'Supporting' and 'regulating' services were provided predominantly by the un-grazed, 'provisioning' and 'cultural' services by the extensively grazed grassland. Secondly, the impact of short sward cattle grazing on the abundance, composition and diversity of the ground dwelling invertebrate community of an upper salt marsh was assessed using pitfall traps (Chapter 4). The findings showed that both cattle grazed and un-grazed saltmarsh habitat should be maintained to maximise invertebrate abundance and diversity and provide suitable habitat for coastal specialists. Thirdly, greenhouse gas emissions from grazed and un-grazed salt marsh were measured monthly for one year. Additionally, below-ground gas sampling tubes were used to measure soil methane concentrations (Chapter 5). Carbon dioxide efflux was greater from the un-grazed marsh soil but 'hotspots' of methane efflux were only found on the grazed marsh. Finally, the influence of grazing on the soil microbial community of both salt marsh and sand dune grasslands was measured by microbial biomass (fatty acid phospholipids: PLFAs), bacterial growth rate (Leucine incorporation) and respiration rates (Chapter 6). Microbial biomass, PLFA markers and bacterial growth rate were all influenced by grazing management. In summary, this work concludes that grazing management clearly affects biological and physical habitat characteristics, biodiversity, ecosystem function and ecosystem service delivery (Chapter 7). Management of coastal grasslands evidently involves trade-offs between biodiversity conservation and multiple ecosystem service provision.

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Chapter 1: Thesis introduction

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1.1 Overview

Coastal grasslands, such as salt marshes and sand dunes, provide many important ecosystem services including carbon storage, coastal protection and recreation. Historically, both grassland habitats were commonly used as agricultural livestock grazing land. Currently, some of these coastal grasslands are 'conservation grazed' (i.e. extensively grazed to maximise plant diversity and to provide a suitable habitat for over-wintering bird species), others have been 'abandoned' (i.e. large herbivores removed) due to the removal of agricultural subsidies or remain historically 'un-grazed'. Grazing management of coastal grasslands influences biological and physical habitat characteristics, ecosystem function, biodiversity and ecosystem service delivery. Understanding the impact of grazing is therefore vital to enable future robust management recommendations. Despite key ecological differences in the two study habitats (salt marshes: high productivity – low plant diversity; sand dune grasslands: low productivity – high plant diversity) I hypothesise that (i) grazing intensity will have a common directional effect on ecosystem characteristics, biodiversity and ecosystem function for both habitats, (ii) that this in turn will influence final ecosystem service delivery leading to management trade-offs.

1.2 Thesis outline

The thesis is divided into seven chapters, and is presented as one review (Chapter 2; not submitted), a series of four experimental research papers (Chapters 3-6) and an overall thesis discussion (Chapter 7) including a saltmarsh field site salinity map (Appendix 7.4). The review chapter investigates a current research question 'Does biodiversity underpin ecosystem service provision?' in relation to two coastal habitats, salt marshes and sand dunes. All four experimental chapters are concerned with the impact of grazing management on temperate upper salt marshes and fixed dune grasslands. Firstly, how grazing management affected ecosystem service provision of sand dune grassland was examined, by measuring a wide range of biophysical variables as proxies for ecosystem services (Chapter 3). Secondly, the impact of short sward cattle grazing on the abundance, composition and diversity of the ground dwelling invertebrate community of an upper salt marsh was assessed using pitfall traps (Chapter 4). Thirdly, greenhouse gas emissions from grazed and un-grazed salt marsh were measured using dark static chambers, monthly for one year. Additionally, below-ground gas sampling tubes were used to measure soil methane concentrations (Chapter 5). Finally, the influence of grazing on the soil microbial community of both salt marsh and sand dune grasslands was measured by microbial biomass (fatty acid phospholipids: PLFAs) and bacterial growth rate (Leucine incorporation), with links made to nutrient cycling (Chapter 6). The thesis discussion draws conclusions on the effect of grazing management on biological and physical habitat characteristics, biodiversity, ecosystem function and ecosystem service delivery for both salt marsh and sand dune habitats (Chapter 7). The trade-offs between management for maximum biodiversity and each set of ecosystem services will also be considered.

1.3 Aims

- Assess the relationship between biodiversity and ecosystem service provision in salt marshes and sand dunes (Chapter 2)
- Record the impact of grazing on sand dune and salt marsh plant and invertebrate diversity (Chapters 3 & 4)

- Find suitable proxies for ecosystem services from measureable biophysical variables (Chapter 3)
- Understand how grazing management influences ecosystem service provision of a coastal grassland (Chapter 3)
- Determine how grazing effects salt marsh regulating service of 'equable climate' (Chapter 5)
- Report how grazing influences microbial composition, activity and the supporting service of 'nutrient cycling' in saltmarsh and sand dune grasslands (Chapter 6)
- Provide a consensus view of grazing management and biodiversity – ecosystem service trade-offs in two contrasting coastal habitats (Chapter 7)

1.4 Contribution of authors to each chapter

Chapters 1, 2 and 7 are entirely my own work and have not been submitted for publication. Chapters 3 – 5 are pre-publication versions of three first author papers with other contributing authors, Angus Garbutt, Laurence Jones & Davey Jones, listed in chapter headings as they appear in the publishing journal. Chapter 6 is a modified version of a joint first author paper, with Johannes Rousk, accepted by Biology and Fertility of Soils. Johannes Rousk undertook the phospholipid fatty acids (PLFAs) and bacterial growth rate measurements. I carried out all the analysis for both journal and thesis versions. We were equally responsible for the written text in the journal version but I wrote > 90% of text for the thesis version. A hyperlink to each published research paper has been provided on the title page for Chapter 3-6.

Chapter 2: Does biodiversity underpin ecosystem service provision in temperate salt marshes and sand dunes? – A review

Hilary Ford

2.1 Introduction

Biodiversity is often used as an indicator of ecosystem health and ecosystem service provision with conservation priorities allocated accordingly (Egoh *et al*., 2007; United Nations Environment Programme: UNEP, 2010; Norris *et al*., 2011). It is therefore vital to critically assess just how important biodiversity is to the provision of ecosystem services within a wide range of habitats. Ecosystem services are the benefits people obtain from ecosystems (Millennium Ecosystem Assessment: MA, 2005; Boyd & Banzhaf, 2007), commonly divided into 'supporting services' (soil formation, primary productivity and nutrient cycling), 'provisioning services' (fresh water supply, food, fibre, timber and fuel products, bio-chemical or genetic resources), 'regulating services' (equable climate, pollution control, flood prevention, invertebrate pollination and pest regulation) and 'cultural services' (recreation, education and aesthetic appreciation) and valued at US$ 16-54 trillion per annum in the 1990s (Costanza *et al*., 1997). Over sixty percent of the world's ecosystems are degraded or over-used, and with the global economy and human population set to increase over the foreseeable future, this trend is likely to continue with a negative effect on ecosystem service provision (Kettunen & Brink, 2006; Chapman, 2008; UNEP, 2008). It is therefore crucial for both scientists and policy makers to work effectively together on ecosystem service projects to provide evidence-based management recommendations for biodiversity conservation and for the

delivery of ecosystem services (Bonte & Hoffman, 2005; Sutherland *et al*., 2006; Ruffo & Kareiva, 2009).

It is commonly stated that biological diversity is key to ecosystem service provision (Convention on Biological Diversity: CBD, 2000). However, the explicit role biodiversity plays in the provision of ecosystem services remains unclear (Hooper *et al*., 2005; Norris *et al*., 2011). What is clear is that both biotic and abiotic factors influence ecosystem service provision. Biotic factors such as biodiversity, functional diversity and functional composition may influence ecosystem service delivery, and are underpinned by abiotic factors such as soil pH, nutrient status, redox potential, temperature, moisture content and vegetation structure.

2.2 The theory - biodiversity measures and ecosystem function

'Biodiversity' is formally defined as 'the variability among living organisms from terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part including diversity within species, between species and of ecosystems' (CBD, 1992). However, in practice biodiversity is often measured using either species richness (number of species present within a community), species evenness (relative abundance of individuals of each species within a community) or indices such as the Shannon index that incorporate both diversity and abundance of species (Gaston & Spicer, 1998; Tilman & Lehman, 2001). Both 'the rivet hypothesis' (Ehrlich & Ehrlich, 1981) and 'the diversity-stability hypothesis' (Chapin *et al*., 2000) provide a theoretical basis for the value of biodiversity to ecosystem function. In brief, each species may react in a different way to an unfavourable event, such as a drought or disease outbreak, thus all should be protected under the precautionary principle, providing greater ecosystem resilience. These theories form the basis of the 'biodiversity-ecosystem function hypothesis' that states that a reduction in biodiversity will cause a reduction in ecosystem level processes (Srivastava & Vellend, 2005), defined as supporting services in the MA (2005). Isbell *et al*. (2011) illustrated this argument by analysing data from 7 biodiversity experiments and concluding

that 84 % of 147 grassland plant species promoted ecosystem functioning at least once. Despite this, functional diversity or functional composition may be more important than biodiversity *per se* as outlined by Walker (1992) in the 'redundant species hypothesis'; as most species are redundant in their roles, only minimal diversity is necessary for proper ecosystem functioning.

'Functional diversity' often focuses on the plant community and can be defined in two ways. Firstly as 'functional group richness' where plants are divided into well established functional types, that often conveniently coincide with taxonomy, e.g. nitrogen (N) fixing legumes, non leguminous forbs, C_3 or C_4 grasses, shrubs and trees (Wright *et al*., 2006). Secondly, as 'the range of functional traits possessed by the biota of an ecosystem' (Diaz & Cabido, 2001). Where each plant species is classified according to a set of functional traits, either 'functional response types', for example drought or frost resistance, grazing tolerant or intolerant, or 'functional effect types' that affect ecosystem processes such as N fixers or ecosystem engineers (Diaz & Cabido, 2001). Ecosystem engineers are species that physically change biotic or abiotic materials and therefore control resource availability to other species (Lawton, 1994; Jones *et al*., 1997). 'Functional composition' refers to the presence (or absence) of certain plant functional types or traits (Diaz & Cabido, 2001). The functional characteristics of dominant species, keystone species or ecological engineers may be crucial for ecosystem functioning (Hooper *et al*., 2005). Ecosystem function and processes are more-or-less equivalent to supporting services.

Both biotic and abiotic factors underpin the diversity of all groups of organisms particularly microbes, invertebrates and plants. Soil microbial diversity may be driven by soil heterogeneity (Young *et al*., 1998; Bardgett *et al*., 2005) or intermediate levels of productivity and disturbance (Rainey *et al*., 2005). Invertebrate diversity may be driven by botanical composition, habitat structure or sward height, soil moisture, temperature and food supply (Curry, 1994). Plant species richness is often explained by the underlying productivity of an ecosystem, a hypothesised hump-backed relationship with biodiversity peaking

at intermediate levels of ecosystem productivity (Grime, 1973; Gough *et al*., 2000; Mittelbach *et al*., 2001).

2.3 Wider evidence - biodiversity measures, ecosystem function and multiple ecosystem service provision

The likelihood of biodiversity, functional diversity or functional composition of an ecosystem influencing ecosystem service provision depends on the ecosystem service under consideration, ecosystem type and the way in which biodiversity is measured. For example, most studies focus on supporting services that are easy to quantity such as primary productivity and aspects of nutrient cycling. Furthermore, the vast majority of biodiversity - ecosystem service research is from grassland habitats using plant diversity as a proxy for total ecosystem biodiversity (Balvanera *et al*., 2006). In addition, research focusing on one particular ecosystem function or service and its relationship to biodiversity may underestimate the diversity required to sustain a multi functional ecosystem (Hector & Bagchi, 2007). There is also a need for caution, if ecosystem service protection is put forward as the main reason for biodiversity protection then any evidence of ecosystem services being provided by low diversity habitats may lead to less support for nature conservation (Ridder, 2008).

There are several examples of an overlap between biodiversity and multiple ecosystem service provision (Odling-Smee, 2005). These associations, however, do not necessarily indicate causality. Where areas of priority biodiversity conservation were compared to areas providing major ecosystem services a positive association between the two was seen for the provisioning service of fresh water, regulating services of carbon (C) storage and flood control, and the cultural service of outdoor recreation (Marxan model - Chan *et al*., 2006). Biodiversity and provision of ecosystem services such as pollination, C sequestration, water quality and tourism were also highly correlated in Oregon, USA (Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) model: Nelson *et al*., 2009). Scenarios that enhanced biodiversity conservation also

enhanced production of ecosystem services. Balvanera *et al*. (2006) presented a meta-analysis of the relationship between biodiversity and ecosystem functioning using data from experimental studies over the past fifty years. They analysed 446 measures of biodiversity effects, 252 from grasslands, 319 of which involved plant manipulations or measurements. They found that increasing biodiversity at one trophic level generally increased productivity, a key supporting ecosystem service, at that level. Plant diversity also appeared to enhance below ground plant and microbial biomass, leading to an increase in decomposer activity. The BIODEPTH project examined plant diversity and ecosystem properties in eight grassland plots across Europe (Hector & Bagchi, 2007). As more ecosystem processes or supporting services such as primary productivity and decomposition or nutrient cycling, were included in their analysis, more species were found to affect overall functioning. Srivastava & Vellend (2005) compiled one hundred biodiversity and ecosystem function studies, half from grasslands and many from mesocosm experiments, and found that 71 % found a positive effect on diversity on at least one ecosystem function such as primary productivity, decomposition or invasion resistance.

There is also evidence of a relationship between functional diversity or composition and ecosystem function or service provision. MacGillivray *et al*. (1995) showed that the difference between plant communities in response to burning, drought and frost were linked to functional plant traits not plant diversity. Mokany *et al*. (2008) found that mean functional trait values of plants explained a larger proportion of variation in five out of eight ecosystem services than either species diversity or functional diversity. Fornara & Tilman (2008) demonstrated that in grassland plants, plant functional complementarity, such as the planting of C_4 grass and legume combinations increased the regulating service of C sequestration via a greater accumulation of soil C. Diaz & Cabido (2001) looked at 24 mainly grassland systems where species richness, functional richness and functional composition were related to ecosystem processes. Functional composition was most likely to influence supporting services such as above-ground primary productivity. The introduction of an invasive species is a

common way in which functional composition is altered, with potential implications for ecosystem service provision. Most ecosystem services rely more on functional composition than either biodiversity or functional diversity (Wall *et al*., 2004; Phoenix *et al*., 2008; De Deyn *et al*., 2009; Lavorel & Grigulis, 2012).

2.4 Selected habitats – salt marshes and sand dunes

Salt marshes (Figure 2.1) and coastal sand dunes (Figure 2.2) were chosen as model habitats for this thesis for three reasons. Firstly, as they are examples of semi-natural systems where diversity is seen as a 'good' or 'natural' aspect worthy of conservation (Jones *et al*., 2011), particularly in salt marshes monitored following managed realignment (Garbutt & Boorman, 2009). Secondly, as coastal habitats they have the potential to provide both terrestrial and marine ecosystem services. Thirdly, despite the fact they often occur alongside each other and are examples of successional habitats they vary enormously in terms of productivity, diversity, potential ecosystem service provision and available scientific literature. Salt marshes are characterised by high productivity, low botanical diversity, quantified ecosystem service provision and plentiful scientific literature (Adam, 1990; Vernberg, 1993; Zedler & Kercher, 2005). Sand dunes, in contrast, are typified by low productivity, high botanical and invertebrate diversity, and a largely un-quantified potential to provide ecosystem services, partly due to the predominance of published sand dune research within grey literature as opposed to peer-reviewed journals (Everard *et al*., 2010).

Salt marshes, along with beaches and mudflats, occur in the temperate coastal intertidal zone (Figure 2.3), whereas in tropical or sub tropical intertidal zones mangrove ecosystems predominate (Vernberg, 1993; Mitsch & Gosselink, 2000). They develop where the shore has sufficient shelter to ensure the build up of sediment from either rivers or the reworking of coastal shelf sediment. Salt marshes are highly productive, successional, vegetated habitats characterised by anaerobic conditions during tidal inundation, fluctuating salinity linked to variable fresh water and salt water inputs and daily and

seasonal fluctuations of temperature (Mitsch & Gosselink, 2000). Salt marshes are often typified by low plant diversity, increased slightly with elevation and grazing management (Daan *et al*., 2002). Upper and therefore drier zones of saltmarshes share some characteristics of semi-natural grasslands, such as the presence of particular grass species also characteristic of terrestrial grasslands and the occurrence of some generalist grassland invertebrates.

Figure 2.1 Dyfi estuary salt marsh, Wales.

Coastal sand dunes occur at all latitudes from the poles to the tropics (Figure 2.3) but this review deals only with those that fall within the temperate zone. Sand dunes form where there is a plentiful supply of loose, sandy sediment that is transported inland by the wind. They form adjacent to sandy beaches above the storm water level and include the dunes themselves and dune slacks, sunken areas between dunes that are flooded in winter and spring (Martínez *et al*., 2004). Coastal dune systems, like salt marshes, are successional habitats characterised by particular stresses. Foredune plants need to be capable of withstanding strong winds, salt spray and sand burial. Further inland succession begins with sand tolerant grasses and forbs (Wiedemann & Pickart, 2004). Dune

systems tend to be lacking in nutrients such as N, phosphorus (P) and potassium (K) leading to low productivity (Willis, 1989). Partly as a result of these stresses, coastal sand dunes are noted for exceptional plant diversity. For example, sand dunes in the Netherlands contain 66 % of all recorded Dutch flora (de Vries *et al*., 1994). This high species richness may be due to the wide range of ecological niches present within a dynamic dune system (Willis, 1989). Low levels of nutrients such as N also allow survival of many stress tolerant plants (Packham & Willis, 1997). Fixed dune grasslands share some characteristics of other high diversity semi-natural grasslands (Bullock *et al*., 2011).

Figure 2.2 Newborough Warren coastal sand dunes, Wales.

Coastal habitats such as salt marshes and sand dunes are at risk from habitat change, over exploitation, invasive species, pollution and climate change (Martínez *et al*., 2004; MA, 2005). They are therefore in need of effective protection and management. These habitats are often converted to land for agriculture, forestry, golf courses, housing developments and tourism (Dijkema, 1990; French, 2001; Martínez *et al*., 2004). Both habitats are also vulnerable to coastal erosion, particularly where the construction of sea defences interferes

with sand or sediment supplies (Lee, 2001). Exploitation for ground water, oil, gas or sediment or sand removal also threatens coastal marshes and dunes (French, 2001; Kennish, 2001). The introduction of non-natives such as *Spartina anglica* for coastal defence has altered the natural communities of many salt marshes (Gedan *et al*., 2009). Invasive wetland species tend to form a tall monoculture leading to a decrease in both plant and animal biodiversity, an increase in productivity and litter and changes in nutrient cycling (Zedler & Kercher, 2004). N and P pollution of salt marsh systems has been common over recent decades (Bakker *et al*., 1993). Nutrient enrichment may increase production of vegetation, decrease species richness and lead to eutrophication (Zedler & Kercher, 2005). Most sand dunes in the UK exceed the critical N load of 10 kg N ha^{-1} $year^{-1}$ due to atmospheric N deposition (Grootjans *et al*., 2004; JNCC 2004; Jones *et al*., 2004). N addition to dune grasslands tends to increase grass and reduce legume biomass (de Vries *et al*., 1994; Heijden *et al*., 2008). Climate change leading to sea level rise and an increase in temperature or carbon dioxide (CO_2) levels could alter both salt marsh and sand dune habitats (Pye, 1998; IPCC, 2007).

Coastal dune habitats are considered a 'priority habitat' and salt marshes a 'general habitat in need of conservation' under annex I of the EU Habitat Directive (1992). In the US, state laws preserve salt marshes (Vernberg, 1993). Salt marsh and sand dune management, in common with other semi-natural grassland habitats, focuses on biodiversity management, particularly for plants and breeding birds, and specific ecosystem services such as flood defence as opposed to general ecosystem service provision (Hofstede, 2003; Jones *et al*., 2011). Until the 1980s, the majority of coastal dunes throughout Europe were managed in line with 'stabilisation' policies. Dunes were often stabilized via marram grass, scrub or tree planting. However, management has now shifted towards a more 'dynamic approach' involving grazing and scrub cutting (Houston, 2005).

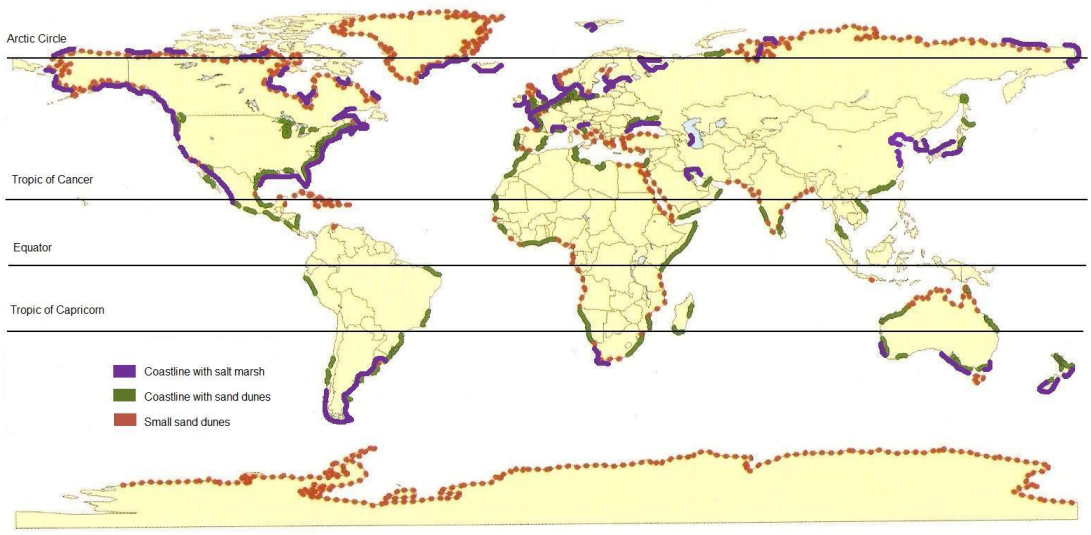

Figure 2.3 Salt marsh and sand dune distribution, based upon Long & Mason (1983), Yang & Chen (1995) and Martínez *et al*. (2004).

2.5 Ecosystem services of salt marshes and sand dunes

Salt marsh and sand dune habitats provide a wide variety of ecosystem services. Ecosystem service provision will be assessed using the framework of the MA (2005). The evidence relating to the influence of 'biodiversity', 'functional diversity' or 'functional composition' on service provision will be considered, as summarised in Table 2.1. Salt marshes are very important for ecosystem service delivery as they link land, freshwater habitats and the marine environment. Salt marshes provide 'supporting services' (soil formation and nutrient cycling), 'provisioning services' (grazing land, haymaking, edible plants, fish and shellfish, salt and chemical production), 'regulating services' (flood and erosion control, improvement of water quality, C sequestration) and 'cultural services' (recreation and education) (Adam, 1990; Vernberg, 1993; Levin *et al*., 2001; Zedler & Kercher, 2005; Gedan *et al*., 2009). Sand dune ecosystem service provision has been less well studied. But Jones *et al*. (2011) have identified several important ecosystem services such as soil formation, flood prevention and recreation.

2.5.1 Supporting services

Evidence relating to three supporting services was reviewed: soil formation, primary productivity and nutrient cycling. Salt marshes and sand dunes are both successional habitats with the ability to build up and stabilise soil. Soil formation is essential as without it other services such as nutrient cycling, climate regulation via soil C storage and flood prevention would not be possible. The formation of soil is dependent on soil biota (European Academies Science Advisory Council; EASAC, 2009), an incredibly diverse group (Young *et al*., 1998), but it is difficult to directly relate microbial diversity to soil formation. Soil formation is linked to soil stability. The stabilization of salt marsh and sand dune sediment or soil relies on microalgal, bacterial, fungal and plant root exudates, and the physical structure provided by root hairs and algal, fungal and mycorrhizal filaments (Packham & Willis, 1997; Read, 1989; Underwood, 1997; Underwood, 2000). Waid (1999) argues that 'metabiosis' the theory that one functional group modifies the environment for another functional group, increases soil biodiversity and leads to stabilised, functioning soil communities.

Primary productivity is fundamental to all other ecosystem services (EASAC, 2009). Salt marshes are among the most productive habitats in the world (Vernberg, 1993; Mitsch & Gosselink, 2000; Figure 2.4). Sand dunes, in comparison, are low productivity systems. Plants tend to be viewed as the main primary producers, however within salt marshes microphytobenthos, seaweed and phytoplankton are also important (Simas & Ferreira, 2007) and in sand dune habitats the algal or microbial mats present in dune slacks also contribute to primary productivity (Vázquez, 2004). Callaway *et al*. (2003) experimentally planted an area of restored Californian salt marsh with 0, 1, 3 or 6 species of salt marsh plants. They found that communities containing 6 species were most productive, based upon biomass measurements. However, *Salicornia virginica*, when planted alone was comparably productive to multi species plots. C_4 plants such as *Spartina anglica*, a common invasive plant species, also tend to photosynthesize rapidly and produce more biomass than native communities dominated by species such as *Juncus gerardii* or *Festuca rubra* (Bakker *et al*.,

1993; Packham & Willis, 1997). Even the C_3 invasive species of European salt marshes, *Elytrigia athericus*, had significantly higher annual net primary productivity than the original, more diverse, plant communities (Valery *et al*., 2004). It is very difficult to find evidence of how plant diversity influences primary productivity in sand dunes, but the evidence from salt marshes suggests that functional composition may be more important for the supporting service of primary productivity than biodiversity.

Figure 2.4 'Supporting service', productive salt marsh habitat, Condor Green marsh, UK.

Nutrient cycling (of N), often measured via the mineralisation of nitrogen by the soil microbial community, is important as it determines plant available nitrogen in most habitats, a limiting factor for plant primary productivity (Bardgett *et al*., 2011). Decomposition may influence nitrogen cycling positively or negatively, dependent on the C:N ratio of organic matter substrate available to microbes (Bardgett, 2005). Decomposition in all soil types, including salt marsh and sand dune, is carried out by a diverse detrital food web of fungi, bacteria and soil fauna (Hopkins & Gregorich, 2005; Setälä *et al*., 2005). In fertile conditions where plants tend to allocate a large proportion of their C resources to rapid

growth, the litter produced tends to be high in nitrogen favouring a bacterial based food web and rapid cycling of nutrients. In less fertile conditions, litter tends to contain a lower proportion of N, fungi are more able than bacteria to break down this substrate, so a slow cycling fungal based food web develops (Wardle, 2005). Soil fauna detritivores, mainly nematodes, mites and collembola, fragment plant litter whilst feeding on the microflora of fungi and bacteria present on the litter surface (Schowalter, 2006). Breakdown of organic matter is rapid in a healthy mature salt marsh; in contrast, detritus in anaerobic water-logged salt marsh soil decomposes more slowly (Brady & Weil, 1996; Hazelden & Boorman, 1999). Coastal dunes tend to be characterized by a fairly low level of decomposition (Kooijman, 2004). As earthworms were only recently discovered to be part of the decomposer community of coastal dunes, this illustrates how little is known about the dynamics of the decomposer community in this habitat (Chamberlain & Butt, 2008).

Wardle (2005) developed the hypothesis that as plant diversity increases, litter diversity and root exudate diversity will also increase, leading to a rise in decomposer diversity. Buth (1987) studied root decomposition in Dutch salt marshes using litter bags. He found that the more species rich root mix from *Puccinellia maritima* community decomposed more rapidly than monoculture stands of *Atriplex portulacoides* or *Spartina anglica*. Decomposition rate may also be influenced by type of dominant vegetation and presence or absence of invasive species, with high lignin content and low N content indicative of slow decomposition (Hemminga & Buth, 1991; Koojiman, 2004; Valery *et al*., 2004). For the soil detritivore community, soil microcosm experiments indicated functional dissimilarity amongst detritivore species was positively correlated with leaf litter loss (Heemsbergen *et al*., 2004). Plant species composition, chemical composition of plant litter, microbial abundance and detritivore type are probably more likely to alter decomposition rates than species richness or functional diversity *per se*. The importance of microbial diversity to nutrient cycling is largely unknown but various molecular techniques involving rRDA, rDNA and analysis of phospholipid fatty acids (PLFAs; Chapter 6) are being

increasingly used in an attempt to answer this question (Torsvik & Øvreas, 2002), by linking taxonomic or functional microbial groups to specific soil processes (Bardgett, 2005).

2.5.2 Provisioning services

Evidence for three provisioning services was reviewed: fresh water, food & materials, and bio-chemicals & genetic resources. Salt marshes, as saline inter-tidal environments, do not provide fresh water. Sand dunes, however, accumulate ground water and can be a potential source of fresh water. Fresh water can be used for drinking and irrigation. Most notably, The Amsterdam Water Supply Dunes of The Netherlands have been managed as a drinking water catchment area since 1874 (Meulen *et al*., 2004).

Salt marshes provide livestock grazing land for provision of lamb and beef (Bouchard *et al*., 2003; Doody, 2008; Figure 2.5) and nursery grounds for fish such as mullet and sea bass (Mathieson *et al*., 2000; Veiga *et al*., 2006). Marsh plants such as Salicornia europaea may also be collected and eaten (King & Lester, 1995). Salt marshes were also traditionally used for turf cutting, salt pans and provision of hay, thatch and rope (Adam, 2000; Bouzille *et al*., 2001). Sand dunes are used for grazing, commercial forestry or opportunistic wild food collecting (Everard *et al*., 2010). Historically, machair, the coastal grassland confined to north-west Scotland and north-west Ireland, was used for crops and grazing, and marram grass was used for animal bedding, basket weaving and thatching (Angus, 1998; Power *et al*., 1998). Most products such as food or fibre harvested from salt marshes or sand dunes are more likely to be influenced by presence of particular species than biodiversity, particularly in the short term. At present bio-chemicals and genetic resources are not provided by salt marshes and sand dune habitats but certain coastal species are currently under investigation e.g. Sea holly *Eryngium maritimum* for biomedical use (Everard *et al*., 2010; Jones *et al*., 2011). As sand dunes in particular are diverse habitats there is potential for exploiting this service in the future.

Figure 2.5 'Provisioning service', sheep grazing at Ynys Hir marsh, UK.

2.5.3 Regulating services

Four regulating services were investigated: climate regulation, pollution control and detoxification, flood prevention, and pollination and pest regulation. Climate regulation refers to the capacity of ecosystems to regulate levels of greenhouse gases such as CO_2, methane (CH_4) and nitrous oxide (N_2O) (EASAC, 2009). Soils store three times as much carbon as vegetation and are therefore important in terms of reducing carbon fluxes to the atmosphere (Fitter, 2005; Hopkins & Gregorich, 2005). Because of their high rates of carbon sequestration and low CH_4 emissions, salt marshes could be very valuable C sinks (Choi & Wang, 2004; Hussein *et al*., 2004). It is known, however, that specific wetland plant species such as *Juncus* (rushes) vent CH_4 via their aerenchyma into the atmosphere (Adam, 1990; Roslev & King, 1996; Chapter 5). The greenhouse gas fluxes of sand dune habitats have not been reported, although as dunes are successional habitats C accumulation is high (Jones *et al*., 2008; Jones *et al*., 2011). It is largely unknown how climate regulation is influenced by biodiversity. It is more likely that the moisture content, temperature, salinity and

composition of plant community within salt marsh or sand dune soils will be more important to greenhouse gas fluctuations than biodiversity.

Salt marshes may improve water quality by acting as a sink of excess nutrients such as N and P and pollutants such as herbicides, pesticides and heavy metals (Jickells *et al*., 2003; Defra / EA, 2005; Alvarez-Rogel *et al*., 2006; Andrews *et al*., 2008). While wetland sediments can act as a sink for certain metals, plants may transform them to a more bio-available form, making metals available to other organisms in the food chain (King *et al*., 2002; Hwang *et al*., 2008). Even if plants are effective in sequestering metals in the short term, after the plant dies the metals may become available again to detritus feeders (Weis & Weis, 2004). It is often assumed that wetlands provide the best nutrient removal service where diversity is low and invasive species or fast growing native species dominate (Zedler & Kercher, 2005). Most studies have focused on the comparison of a limited number of species, usually the dominant native and the invasive species. A mesocosm experiment carried out by Herr-Turoff & Zedler (2005) compared grassland communities with and without the invasive species *Phalaris arundinacea* and found that both were equally effective in removing N from discharged water. Weis & Weis (2004) found that *Phragmites australis*, an invasive species in the US sequesters more metal in its roots and releases less via leaf excretion than the native *Spartina alterniflora*. In addition, Ravit *et al*. (2005) found that *S. alterniflora* is more likely to make a specific flame retardant chemical more bioavailable than *P. australis* due to the greater surface area of *Spartina* roots providing an increased habitat for microbial communities that include those that biotransform contaminants. One particular salt marsh plant, *Atriplex portulacoides*, appears to be more mercury tolerant than other salt marsh species, it retains mercury in root cell walls, effectively immobilizing it (Valega *et al*., 2009). Functional composition of plants and the microbial community seem much more important to the provision of pollution control and detoxification than biodiversity.

Coastal ecosystems such as salt marshes and sand dunes are very important for flood control as they form a physical barrier between the land and the sea

(French, 2001; Doody, 2008; Jones *et al*., 2011; Figure 2.6). Saltmarshes are around 30 % more effective at dissipating wave energy than mud flats due to the presence of vegetation (Möller *et al*., 1999; Möller *et al*., 2001; Cooper, 2005). Height, flexibility or leaf pattern of macrophytes are important for wave attenuation. For example, *Spartina anglica* was shown to dissipate wave energy three times more than *Zostera anglica* due to the stiffness of *Spartina* leaves, this is more likely to do with physical characteristics than species diversity (Bouma *et al*., 2005). In addition, the value of coastal protection afforded by salt marsh vegetation is likely to vary seasonally, especially if storms occur when plant biomass or density are low (Koch *et al*., 2009). Many coastal dunes in North America and Europe were planted with marram grass, *Ammophilia arenaria*, in place of the natural flora of the foredune, for stabilisation and flood prevention (Wiedemann & Pickart, 2004). Vegetation type and structure, as opposed to biodiversity, are more likely to influence the regulating service of flood prevention.

Figure 2.6 'Regulating service' of flood prevention, Glasson marsh, UK.

Invertebrates are very important for the provision of pollination and pest regulation (Losey & Vaughan, 2006). Although salt marshes and sand dunes are not used for commercial crop production, these habitats provide a refuge for a range of invertebrate pollinators and pest control species, such as spiders and carabid beetles that may travel to adjacent agricultural areas. Salt marshes

support an abundant invertebrate community of medium diversity (Chapter 4), whereas sand dunes support a less abundant but more diverse population (Chapter 3). The presence of bee pollinators with different functional traits, related to flower visiting time and behaviour, was found to increase seed set and crop yield in pumpkins (Hoehn *et al*., 2008), and wild bee diversity was linked to effective pollination services for organic crops in California (Kremen *et al*., 2002). Biological control of pests is provided by generalist and specialist predators and parasitoids including spiders, beetles, wasps, nematodes, fungi and bacteria (Beattie & Ehrlich, 2001; Balmford *et al*., 2008). The abundance and diversity of pollinators and invertebrate pest regulators are both likely to be important in the potential provision of this service (Balmford *et al*., 2008).

2.5.4 Cultural services

Cultural services include recreation and tourism, education, conservation, spiritual and aesthetic values (Figure 2.7). These are likely to be enhanced by bio-diverse habitats (Church *et al*., 2011). Salt marshes and sand dunes are important for recreational activities such as bird watching, wildfowling and dog walking, and as educational models of successional habitats. Salt marshes provide habitat for a number of bird species such as redshank, lapwing, oystercatcher, skylark, reed bunting and meadow pipit which use them for roosting, feeding and breeding (Vernberg, 1993; Defra / EA, 2005; Doody, 2008). Vegetation sward height is a more important feature of habitat quality for breeding redshank than the presence of particular plant species (Norris *et al*., 1997). Dune systems also provide valuable habitat for breeding birds and endangered species such as sand lizards, *Lacerta agilis*, and natterjack toads, *Bufo calamita* (Bonte & Hoffmann, 1998; Edmondson & Velmans, 1998). Spiritual values are more difficult to define although sand dunes are important to the Maori of New Zealand (Martínez *et al*., 2004). Visitors to salt marsh or dune habitats may not always value the natural habitat as might be expected. Sefton coast visitors put a greater value on an introduced habitat, pinewoods and their associated red squirrel population than on the 'natural' dune habitat (Edmondson & Velmans, 1998). And within the Meijendel dunes of the

Netherlands visitors rated an 'unnatural' feature most highly, the lakes constructed for drinking water (Meulen *et al*., 2004).

Figure 2.7 'Cultural services' of education, recreation and conservation, a break from soil and vegetation sampling at Crossens marsh, UK.

2.6 Conclusions

Salt marshes are important habitats for the provision of many ecosystem services, primary productivity, pollution control, flood regulation and recreational value in particular (Table 2.1). Soil formation, nutrient cycling, provision of food and fibre and climate regulation services are also provided. Sand dunes are key habitats for soil formation, climate regulation, flood prevention and recreation services. Most ecosystem services, 'supporting', 'provisioning', 'regulating' or 'cultural' rely more explicitly upon functional composition rather than either biodiversity or functional diversity for their delivery. Current evidence highlights two services likely to depend upon biodiversity, the provisioning service of bio-chemicals and genetic resources and the regulating services of pollination and pest control.

Table 2.1 Ecosystem services provided by salt marsh and sand dune habitat (✓ = low, ✓✓ = medium, ✓✓✓ = high, composition = functional composition) following the framework of the MA (2005), information based on results of literature review and Jones *et al*. (2011).

Service	Provision by salt marshes	Provision by sand dunes	Importance of biodiversity	How service could be measured
Supporting				
Soil formation	✓✓	✓✓	Unknown	Amount of top soil formed
Primary Productivity	✓✓✓	✓	Composition	Above and below ground net productivity
Nutrient cycling	✓✓	✓	Unknown / Composition	N mineralisation
Provisioning				
Fresh water		✓	Unknown	Water quantity and quality
Food and materials	✓✓	✓	Composition	Total biomass
Bio-chemicals and genetic resources	✓	✓	Biodiversity potential	Total amount of useful substances that could be extracted
Regulating				
Climate regulation	✓✓	✓✓	Unknown / Composition	Greenhouse gas balance, C stock
Pollution control and detoxification	✓✓✓		Composition	Accumulation of pollutants in sediment
Flood prevention	✓✓✓	✓✓	Composition	Water storage capacity, wave dissipation capacity
Pollination and pest regulation	✓	✓	Biodiversity / Abundance	Abundance of pollinators or pest regulators, distance to arable fields
Cultural services				
Recreation, education and spiritual values	✓✓✓	✓✓✓	Biodiversity	Presence of landscape features, number of visitors

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Chapter 3: Impacts of grazing abandonment on ecosystem service provision: coastal grassland as a model system

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3.1 Abstract

A coastal grassland was used as a model system to examine how grazing management, un-grazed (for six years), rabbit grazed or fully grazed (ponies 0.2 ha^{-1}, cattle 0.05 ha^{-1} and rabbits 45 ha^{-1}), affected biodiversity and ecosystem service provision, by measuring an extensive suite of biophysical variables as proxies for ecosystem services. For 'supporting services', nutrient cycling was greatest in un-grazed grassland but primary productivity did not differ. The 'provisioning service' of food production was only provided by fully grazed grassland. For grazing effects on 'regulating services' total carbon (C) stock did not differ and effects on pest regulating invertebrates and pollinator abundance were variable. The potential for flood control was considered greatest in the un-grazed grassland; with faster water infiltration than in the fully grazed grassland. The 'cultural service' of environmental appreciation was considered higher in fully grazed grassland due to significantly greater plant species richness, more forb species and more forbs flowering than in un-grazed grassland.

Key-words: biodiversity, conservation, ecosystem function, management, semi-natural grassland, trade-offs

3.2 Introduction

Grassland management for multiple ecosystem services often results in potential conflicts or trade-offs (Macleod and McIvor, 2006). This is important as many ecosystem services are delivered by semi-natural grasslands (Bullock et al., 2011; Table 3.1); "supporting services" (primary productivity and nutrient cycling); "provisioning services" (food production, preservation of the genetic diversity of wild species and fresh water supply); "regulating services", (maintenance of an equable climate, water storage, pest regulation and pollination) and "cultural services" (conservation status, environmental appreciation and recreation). In managed grasslands, the basic trade-off is between intensive management to maximise food production and extensive management resulting in lower production, but increased biodiversity and a wider range of cultural services (Power, 2010). Semi-natural, low productivity grasslands, traditionally used for low intensity cattle and sheep farming, have declined by 90 % in the UK since 1945, converted to intensive production by drainage and fertilisation (Bullock et al., 2011). In many parts of Europe they now face a further threat, with managed grazing of these habitats being 'abandoned' in both the uplands and lowlands due to the removal of European Union (EU) subsidies (Strijker, 2005). Policy makers have signed up to halt biodiversity loss and degradation of ecosystem services within the EU by 2020 and to adopt an integrated approach to land use management (Kleijn et al., 2011). It is therefore vital to assess how abandonment of low productivity grazing land impacts on biodiversity, ecosystem function and potential consequences for ecosystem service provision.

The effects of removing large herbivores (i.e. cattle, sheep or horses) are well understood for grassland biodiversity and ecosystem function, but the implications for wider ecosystem service provision have been poorly quantified, or not quantified at all, especially for multiple services (Power, 2010). Grazing removal decreases plant diversity (Pykälä, 2003), increases invertebrate and small mammal abundance and diversity (Morris, 2000; Schmidt et al., 2005), and can either increase or decrease bird abundance and diversity dependent on feeding and nesting sward requirements (Vickery et al., 2001). Where large grazers are removed

smaller grazers, particularly rabbits, may define habitat characteristics, keeping patches of grassland fairly open, preventing declines in plant diversity but allowing soil to become less compact (Isermann et al., 2010), creating a habitat with characteristics of both grazed and un-grazed grassland, with likely mixed effects upon ecosystem services. Voles and other small mammals are usually present, even within 'un-grazed' areas and have different effects on vegetation and nutrient cycling characteristics to large herbivores (Bakker, 2003). Cessation of cattle grazing where rabbits are not present leads to the development of a plant community dominated by highly competitive tall grasses or shrubs (Janišová et al., 2011) with reduced soil compaction and possible implications for several variables linked to ecosystem service provision.

Table 3.1 Ecosystem services (S = supporting, P = provisioning, R = regulating, C = cultural) with list of proxy measurements.

Ecosystem service	Proxy measurement
Primary productivity (S)	Annual net primary productivity (above ground)
Nutrient turnover (S)	N mineralisation rate
	Detritivore feeding rate
	Root turnover rate
Food production (P)	Number of cattle per hectare
Genetic diversity (P)	Plant species richness
Equable climate (R)	C stock
Flood control potential (R)	Water infiltration rate
Pest regulation (R)	Invertebrate biodiversity, spider and predatory beetle abundance
Pollination (R)	Nectar feeder biodiversity and abundance
Conservation (C)	Abundance of RDB or nationally scarce invertebrates
Aesthetic appreciation (C)	Plant biodiversity, vegetation structure, grass: forb ratio & flowering

Above-ground primary productivity (ANPP), a key supporting service, may increase or decrease with grazing intensity (De Mazancourt et al., 1998; Leriche et al., 2003). Nutrient turnover, another supporting service, also shows variable effects with grazing management (Bakker, 2003; Bardgett et al., 1998; Van Wijnen et al., 1999). Coastal grasslands, particularly those adjacent to crop fields, may potentially provide invertebrates for the twinned regulating services of pest control and pollination (Everard et al., 2010; Losey and Vaughan, 2006). However, effects of grazing intensity on these services are difficult to predict. Invertebrate pest

regulators, such as spiders and beetles, are often more abundant on un-grazed grassland (Morris, 2000) but pollinators may be most abundant on grazed grassland due to a likely increase in floral resources (Potts et al., 2003; Sjödin et al., 2008). Soil moisture and temperature changes may also affect the regulating service of equable climate, via impacts upon C storage and greenhouse gas emissions (Luo and Zhou, 2006). The cultural service of aesthetic appreciation is likely to be higher in grazed grasslands due to expected greater plant diversity and abundance and diversity of forbs (Pykälä, 2003).

To date, where links have been drawn between grazing intensity, impact upon ecosystem characteristics, and multiple ecosystem service provision, these have been largely based on literature reviews (Bullock et al., 2011; Kemp and Michalk, 2007). There have been few habitat case studies where these effects have been quantified within an ecosystem services framework. The novelty of this study lies in using a wide range of habitat measurements across different grazing intensities as proxies for specific ecosystem services (Table 3.1). A managed grazing experiment within a low fertility grazed coastal grassland was used as a model system to examine how grazing affects ecosystem service provision, following the framework of the Millennium Ecosystem Assessment (MA, 2005) and the UK National Ecosystem Assessment (Bullock et al., 2011). The three grazing treatments used were 'fully grazed' (i.e. extensively cattle, pony and rabbit grazed), 'rabbit grazed' and 'un-grazed' (i.e. abandoned). The overarching hypothesis of this study is that 'changes in grazing will differentially affect individual services, and will alter the balance of supporting, provisioning, regulating and cultural ecosystem service provision of semi-natural grassland.

3.3 Materials and methods

3.3.1 Study site and experimental design

Fixed sand dune grasslands are low-productivity semi-natural grasslands, and a UK Biodiversity Action Plan (BAP) priority habitat. Newborough Warren is a calcareous coastal sand dune grassland, located in NW Wales (53° 8' 59" N, 4° 21' 1" W), noted for its high biodiversity and designated as a National Nature Reserve, Site of Special

Scientific Interest and Special Area of Conservation under the EC Habitats and Species Directive 1992. The 389 ha site is managed by Countryside Council for Wales (CCW). Managed grazing was introduced in 1987; stocking levels have varied but the site is now grazed by ponies (*Equus ferus caballus*; 0.2 ha^{-1}), cattle (*Bos taurus*; 0.05 ha^{-1}) and rabbits (*Oryctolagus cuniculus*; 45 ha^{-1}), designed to maximise plant diversity. Rare breed cattle, Belted Galloways and Dexters are stocked within the fully grazed study area for 18 months before being 'finished' on improved pasture and sold for meat (Graham Williams, pers. comm.). The predominant vegetation in the experimental area is fixed dune *Festuca rubra* - *Galium verum* grassland. In 2003, three replicate experimental blocks, each containing three 10 x 10 m experimental units, one fully grazed unit (unfenced), one rabbit grazed unit (fenced with 10 x 10 cm mesh to exclude large grazers) and one un-grazed unit (fenced with 10 x 10 cm mesh and an additional 2.7 x 3.7 cm mesh buried 20 cm underground to prevent rabbit access) were set up. Experimental blocks are separated from each other by hundreds of metres and by low dunes. Prior to construction of grazing exclosures the vegetation was a uniform 4-6 cm height. Small mammals such as field voles (*Microtus agrestis*) and invertebrate herbivores were assumed to be present within all experimental units. All biophysical measurements avoided a 1 m buffer zone adjacent to the fences for rabbit grazed and un-grazed exclosures. Fully grazed units are denoted as PR1 - PR3 (PR stands for pony & rabbit grazed); rabbit grazed units as R1 – R3 and un-grazed units as U1 - U3.

3.3.2 Soil characteristics

Soil moisture content and temperature were recorded within each experimental unit, at six locations, once a month from June to September 2009. Soil conductivity was measured in direct volts using a *Delta T* Theta Meter HH1 across 6 cm depth and converted to percentage soil moisture content using a calibration suitable for mineral soils. Soil temperature was measured in the top 11 cm using a digital thermometer. Samples to determine bulk density and soil organic matter content were collected during September 2009 using three intact soil cores of 3.8 cm diameter and 15 cm depth from each experimental unit. Cores were dried at 105 ^{o}C

for 72 h and the dry mass divided by the volume of the core to calculate bulk density. Loss-on-ignition, at 375 ^{o}C for 16 h was used to estimate organic matter content. pH was determined using a Corning pH meter 220. Water infiltration rate was measured using three single ring infiltrometers (Carroll et al., 2004) per experimental unit. This method was used as vertical percolation flux dominates water flow in sandy soil. These 10 cm diameter x 20 cm length cylinders were hammered 5 cm into the ground and briefly filled with water to pre-saturate the ground. Water was again poured into the infiltrometers up to 5 cm from the top. The time taken for the water to move 5 cm down the infiltrometer was recorded and converted into a water infiltration rate in mm min^{-1}.

Plant available nitrogen (N) was measured by N mineralisation assays (Rowe et al., 2011) calculated from three 15 cm depth soil cores per unit, taken in September 2009. Soil cores were taken using plastic corers, capped at both ends to minimise soil disruption and stored intact at 4 °C. Accumulated inorganic N was flushed from the cores by spraying with a solution of similar ionic concentration to UK rain over 7 d until 150 ml of leachate had been collected. Cores were incubated at 10 °C for 28 d, homogenised and a sub-sample extracted using 1M KCl for the analysis of ammonium and nitrate content (Rowe et al., 2011). Net nitrification and ammonification rates were calculated over these 28 d, assuming that all previous inorganic N had been removed during the 7 d flushing period, and were expressed as mg N g^{-1} dry wt d^{-1}. Litter breakdown via mesofaunal detritivores was measured in autumn using ten bait lamina (Terra Protecta GmbH, Germany) per unit (in two lines of five, 50 cm apart).

3.3.3 Vegetation characteristics

During July, vegetation height was measured at five points within five 1 x 1 m quadrats per experimental unit with a custom made drop disc of 20 cm diameter, 10 g mass. Within two quadrats from each unit above-ground live vegetation and plant litter was collected from a 25 x 50 cm area cut to ground-level. One root core of 5 cm diameter and 10 cm depth was also taken per quadrat and washed to remove all soil. Above-ground vegetation, litter and roots were all dried at 80 ^{o}C for

24 h and weighed to give indicators of above-ground shoot biomass, litter biomass and below-ground root biomass respectively. C stock (t C ha^{-1}) was measured for four pools: soil, roots, plant litter and shoots, derived from biomass using the following conversions: Soil C as 0.55 of soil organic matter; root C is 0.44 of root biomass (dry wt) and plant litter and shoot C is 0.42 of biomass (dry wt) in comparable UK fixed dune grasslands (unpublished data). ANPP, peak biomass from three grazer excluded areas per experimental unit, was recorded as a direct measure of primary productivity. During February 2009, vegetation was cut to ground level in three 50 x 50 cm areas per experimental unit. Each cut area was protected from pony, cattle and rabbit grazers by an 8 cm mesh gabion (50 x 50 x 50 cm) and vegetation allowed to re-grow until peak biomass at the end of August when areas were re-cut within a central 25 x 25 cm area. Vegetation was dried at 80 °C for 72 h then weighed and converted to kg dry wt m^{-2} yr^{-1} to provide a measure of ANPP. Autumnal fine root turnover was estimated by modifying the method of Lukac and Godbold (2010). In mid September 2010 four nylon 1 mm root turnover mesh strips (Normesh, UK), 2.5 cm wide x 15 cm long, were placed in vertical cuts made in the soil with 2.5 cm overlap at the bottom and 2.5 cm emerging from the soil, 50 cm apart, across a 2 m transect in each unit. After 28 d the mesh strips were removed along with a slightly wider and deeper intact soil core. Cores were pushed out and divided in two along the mesh line, the number of fine roots penetrating each mesh depth zone (0 – 2.5; 2.5 – 5; 5 – 7.5; 7.5 – 10 cm) were counted by eye as a proxy for fine root turnover.

3.3.4 Biodiversity of plants and invertebrates

Plant percentage cover, species richness and number of species flowering were recorded during July in five 1 x 1 m quadrats from each experimental unit. For functional group analysis, plant percentage cover data was standardised to 100 % and divided into six broad phylogenetic functional groups: lichen, moss, forbs, sedges, grass and shrubs.

Pitfall traps were used to sample ground dwelling invertebrates for 26 d in May and 28 in July. Six pitfall traps per experimental unit were set up in two lines of three, 2

m apart. Each trap consisted of a plastic cup (80 mm diameter x 105 mm deep) a third full with a 50/50 mix of ethylene glycol and water, to preserve invertebrates, with a drop of washing up liquid to break the surface tension. Each trap was pushed into a hole made by a soil auger until they were level with the soil surface. A rain hat was placed over each trap and set at 3 cm from the ground. A wire basket of 5 cm mesh size was also placed over each rain hat and pegged down to prevent interference by grazers. Most invertebrates caught in pitfall traps were identified to species level, apart from Diptera and parasitic Hymenoptera, and assigned to a functional group: predatory, zoophagous (predatory and scavenging), phytophagous (herbivore or granivorous), detritivore (feed on detritus and associated decomposer community of fungi and bacteria), or an additional category 'not assigned'.

Nectar feeding invertebrates were sampled by bait-less pan traps, six per experimental unit (2 blue, 2 white, 2 yellow), for 72 h during June and again in July 2009. In each experimental unit two triangles, 5 m apart, consisting of one pan trap of each colour, 1.5 m apart, was set up. Traps of the same colour were pooled to give three samples per experimental unit. Each trap consisted of 203 mm diameter shallow bowls sprayed yellow, blue or white, half filled with water containing a drop of washing detergent to break the surface tension. Wire baskets of 5 cm mesh size were placed over all traps to prevent damage by grazing animals. The contents of the pitfalls and pan traps were preserved in 70 % Industrial strength methylated spirits (IMS) or ethanol.

3.3.5 Analysis

The effect of grazing on each measured variable was analysed using an ANOVA on linear mixed effects model (lme) output in R (R Development Core Team, 2011) e.g. lme (temperature ~ grazing, random = ~1|block/grazing). This approach was used to enable the raw data to be analysed accounting for replication at the level of the experimental unit or block (n=3). Variables were log, square root, or arcsine square root transformed as appropriate to improve model fit. Results of best model fit were presented here based on lowest Akaike information criterion (AIC) number

and quantile probability plot (qqnorm) with most normal distribution. Where ANOVA results showed a significant grazing effect, differences between pairs of grazing treatments (PR & R; PR & U), were reported directly from the lme summary output. As the remaining treatment pair (R & U) could not be 'read' directly from the lme summary, the difference between values for R and U in relation to PR was divided by the standard error to give a number (#) for the following calculation '2*(1 – pt(#,df=4))' This gives a probability value for the difference between R and U for a two-tailed test where d.f. = 4.

3.4 Results

3.4.1 Soil and vegetation characteristics

Soil temperature was significantly higher on the fully grazed than the un-grazed grassland. Vegetation height was significantly different between all treatment pairs with the lowest sward height in the fully grazed, intermediate in the rabbit grazed and highest in the un-grazed grassland (Table 3.2). Root biomass was significantly greater in the rabbit grazed than the un-grazed grassland. Plant litter was significantly higher in the un-grazed and rabbit grazed compared to the fully grazed grassland. Water infiltration rate, was significantly higher in the un-grazed and rabbit grazed than fully grazed grassland. Soil pH, moisture content, bulk density, organic matter content and above-ground shoot biomass were not significantly different between grazing treatments. Total C stock did not differ significantly with grazing. As separate C pools 'soil' and 'shoots' (above-ground live biomass) were not significantly different between grazing treatments (Figure 3.1). Root C stock was significantly greater for rabbit grazed than un-grazed grassland, contributing around 20 % of the total C pool. Plant litter C stock was significantly greater in un-grazed and rabbit grazed than grazed grassland.

ANPP and soil organic matter content (soil surface organic layer ~6 cm thick) did not differ significantly with grazing treatment (Table 3.2). Net nitrification rate was significantly higher in the un-grazed than the fully grazed grassland but net ammonification rate did not differ significantly with grazing treatment (Figure 3.2). Mesofaunal feeding rate was significantly greater for rabbit grazed in depth zone 1

and for un-grazed in depth zone 2 and 3 compared to fully grazed grassland (Figure 3.3). Fine root turnover at 0-2.5 cm was significantly greater in un-grazed and rabbit grazed than fully grazed grassland (Figure 3.4).

Table 3.2 Soil and vegetation characteristics, grazing treatment means ± standard deviations with bold letters indicating significant differences at *($p < 0.05$) or *($p < 0.001$), *ns* = non-significant.**

	Fully grazed	Rabbit grazed	Un-grazed	ANOVA
Soil				
pH	6.21 ± 0.37	6.16 ± 0.45	6.01 ± 0.33	*ns*
Moisture content (%)[x]	13.02 ± 8.12	8.28 ± 2.62	6.26 ± 5.42	*ns*
Temperature (°C)[x]	18.08 ± 2.90 **a**	17.20 ± 0.39 **ab**	16.93 ± 2.20 **b**	*
Bulk density (g cm^{-3})	1.01 ± 0.07	1.02 ± 0.09	0.93 ± 0.10	*ns*
Organic matter content (%)	3.11 ± 0.71	3.23 ± 0.64	3.57 ± 0.92	*ns*
Infiltration rate (mm min^{-1})	6.60 ± 1.94 **a**	22.74 ± 14.7 **b**	37.27 ± 28.8 **b**	*
Vegetation				
Vegetation height (cm)	5.27 ± 1.03 **a**	19.43 ± 7.68 **b**	37.63 ± 7.94 **c**	***
Root biomass (kg dry wt m^{-2})	1.24 ± 0.55 **ab**	1.22 ± 0.36 **a**	0.71 ± 0.26 **b**	*
Litter biomass (kg dry wt m^{-2})	0.12 ± 0.03 **a**	0.22 ± 0.08 **b**	0.28 ± 0.04 **b**	*
Shoot biomass (kg dry wt m^{-2})	0.83 ± 0.29	0.80 ± 0.29	0.59 ± 0.25	*ns*
ANPP (kg dry wt m^{-2} y^{-1})	0.34 ± 0.09	0.35 ± 0.07	0.34 ± 0.10	*ns*

[x] Mean values of 4 months data, June-September

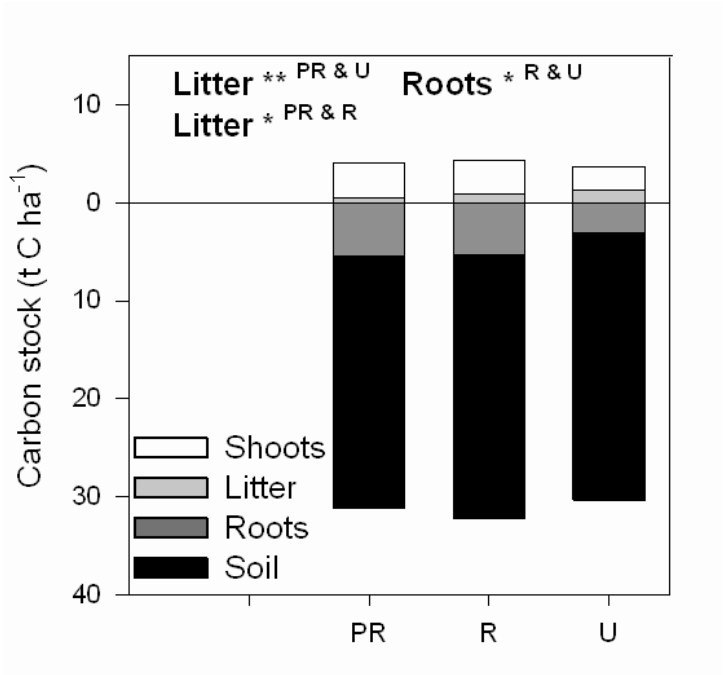

Figure 3.1 Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on C stock. Bold text indicates significant differences between grazing treatments for each component, * (*p* < 0.05), ** (*p* < 0.01).

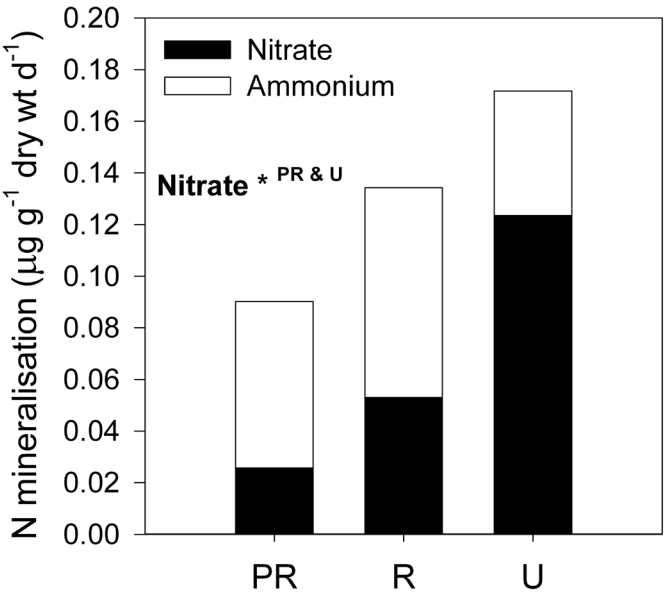

Figure 3.2 Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on N mineralisation. Bold text indicates significant differences between grazing treatments for each component, * (*p* < 0.05).

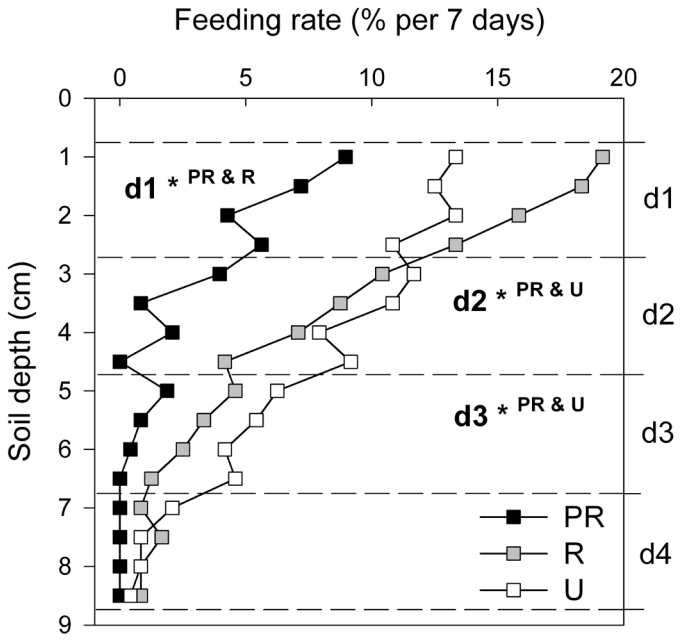

Figure 3.3 Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on below-ground mesofaunal feeding rate in autumn. Bold text indicates significant differences between grazing treatments for each depth zone (d1 – d4), *($p < 0.05$).

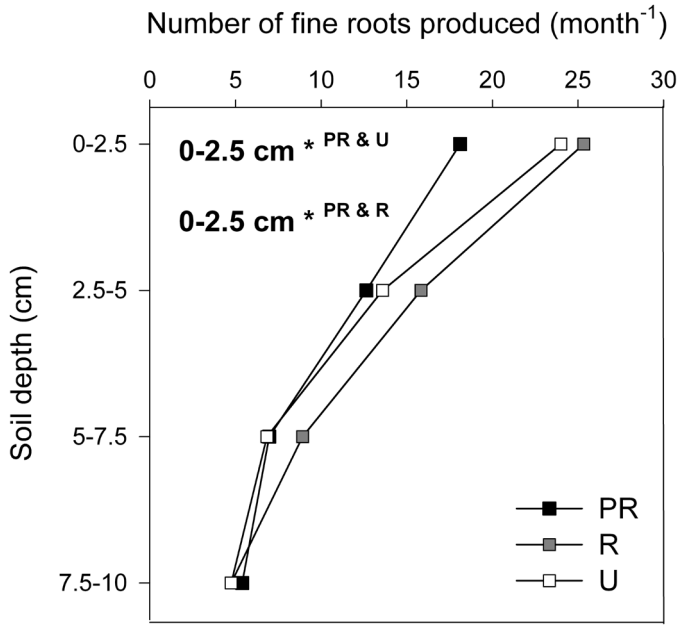

Figure 3.4 Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on number of new fine roots produced per month, as a proxy for potential fine root turnover. Bold text shows significant differences between grazing treatments for each soil depth * ($p < 0.05$).

3.4.2 Biodiversity

Cumulative plant species richness, for un-grazed, rabbit grazed and fully grazed plots was 45, 49 and 61 species (per 15 m^2) respectively. At the experimental unit level, fully grazed grassland was significantly more species rich, particularly for forbs, than un-grazed grassland (Table 3.3). Graminoids were equally species rich regardless of grazing intensity. Forb cover was significantly higher in fully and rabbit grazed grassland than in un-grazed habitat. In contrast, grass cover was significantly lower in fully grazed than rabbit or un-grazed grassland (Figure 3.5). Total number of species flowering, particularly forbs, and percentage of forb species flowering were all significantly greater in fully grazed than un-grazed habitat.

Table 3.3 Plant species richness and flowering, grazing treatment means ± standard deviations with bold letters indicating significant differences at *(*p* < 0.05), *ns* = non-significant.

Variable	Fully grazed	Rabbit grazed	Un-grazed	ANOVA
Mean species richness (spp per 1 x 1 m)				
All species	22.93 ± 4.04 **a**	18.93 ± 4.51 **ab**	16.20 ± 2.27 **b**	*
Graminoid (grasses & sedges)	7.33 ± 1.50	7.20 ± 0.86	6.60 ± 0.83	*ns*
Forb	11.13 ± 2.45 **a**	7.80 ± 2.81 **ab**	5.47 ± 1.36 **b**	*
Number of species flowering				
All species	10.53 ± 3.36 **a**	8.93 ± 2.15 **a**	6.33 ± 1.84 **b**	*
Graminoid	4.40 ± 1.50	5.67 ± 0.98	4.60 ± 1.24	*ns*
Forb	6.13 ± 2.20 **a**	3.27 ± 1.83 **ab**	1.73 ± 1.22 **b**	*
Percentage species flowering				
Graminoid	59.89 ± 16.8 **a**	79.02 ± 11.6 **b**	69.40 ± 16.4 **ab**	*
Forb	54.36 ± 14.6 **a**	41.92 ± 15.1 **ab**	32.29 ± 21.2 **b**	*
Forb / forb + graminoid pc.				
Forb percentage	21.25 ± 0.07 **a**	16.65 ± 0.08 **a**	6.90 ± 0.05 **b**	*

Of nearly ten thousand invertebrates sampled from pitfalls, 40 % were predatory spiders of 62 species and 3 % predatory and zoophagous beetles, mainly carabids and Staphylinidae of 43 species. Pan traps sampled 14 bee species. Predatory Coleoptera were more abundant (ANOVA; F = 5.2, d.f. = 4, $p < 0.05$) and species rich

(ANOVA; F = 13.2, d.f. = 4, $p < 0.01$) in fully grazed than un-grazed grassland. Araneae were also significantly most abundant (ANOVA; F = 9.72, d.f. = 4, $p < 0.05$) and species rich (ANOVA; F = 9.72, d.f. = 4, $p < 0.05$) on fully grazed land. Nectar feeders, as a proxy for pollinators, did not differ significantly in either abundance or species richness with grazing intensity.

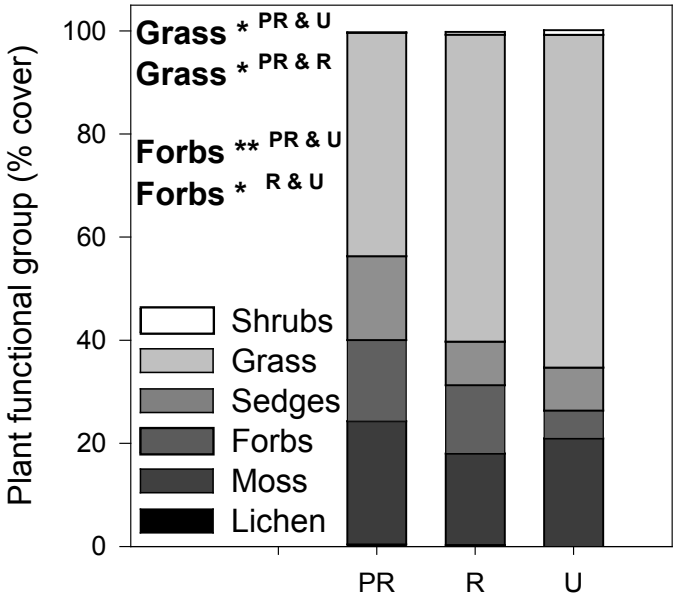

Figure 3.5 Effect of grazing (PR = fully grazed, R = rabbit grazed, U = un-grazed) on plant functional groups (adjusted to 100 %). Bold text shows significant differences between grazing treatments for each plant group, * ($p < 0.05$), ** ($p < 0.01$).

Pan traps sampled *Colletes cunicularius* a Red Data Book (RDB3) listed sand mining bee, and pitfalls sampled the carabid beetle *Amara lucida*, Staphylinidae *Mycetoporus piceolus* and *Mycetoporus punctus*, Linyphiidae *Mecopisthes peusi* and the ground bug *Megalonotus praetextatus*, all nationally scarce invertebrates associated with coastal dune habitat (Alexander et al., 2005). Certain species were only found as one or two isolated individuals, *C. cunicularius*, *A. lucida*, *M. punctus* and *M. praetextatus*, and therefore cannot be linked to habitat type. The rove beetle *M. piceolus* was more abundant in the un-grazed grassland; in contrast the small spider *M. peusi* was more numerous in the grazed grassland. Full results for invertebrate abundance and diversity are presented in Table A3.1.

3.5 Discussion

Most European semi natural grasslands, including coastal grasslands, have suffered a decline in traditional grazing, with marginal grasslands being 'abandoned' or replaced by 'conservation grazing' to address conservation priorities such as plant diversity or provision of habitat for breeding birds (GAP, 2012). The relationships between grazing impacts on biophysical measures in this study and probable impacts on ecosystem services are summarised in Figure 6, supplemented by additional information from the literature for some services. We acknowledge that for some of these services, particularly the cultural services, they are proxies of 'potential' ecosystem services, rather than 'realised' ecosystem services. From the results of this study, it is clear that different grazing regimes favour different ecosystem services, and management decisions necessitate trade-offs in delivery of those ecosystem services, or changes in the way grazing management is applied. Here, the widely held view that low intensity grazing is always the 'best' management option for the conservation of semi-natural grasslands is challenged.

3.5.1 Supporting services

Primary productivity and nutrient cycling are key supporting services of semi-natural grasslands. These underlie regulating services such as equable climate by greater plant biomass leading to higher C sequestration rates (Soussana et al., 2004), and provisioning services such as forage production and quality (Bullock et al., 2011). Nutrient cycling is important as it determines plant available N, a limiting factor for plant primary productivity (Bardgett et al., 2011). Decomposition may influence N cycling positively or negatively, dependent on the C:N ratio of organic substrate available to microbes (Bardgett, 2005). Generally, faster decomposition rates will be detrimental for C storage as soil respiration will increase (Luo and Zhou, 2006). Classic theory suggests that more intensively grazed land will be dominated by faster bacterial nutrient cycling and un-grazed or lightly grazed grassland by slower fungal cycling (Bardgett et al., 1998; McNaughton et al., 1997). However, in this study one aspect of nutrient cycling, net nitrification rate, was greatest in un-grazed grassland, supporting an opposing view that grazing by large

herbivores can decrease nutrient cycling (Bakker, 2003; Van Wijnen et al., 1999). This may be because cattle distribute N unevenly via their faeces and urine whereas smaller mammals such as voles, present within un-grazed units, return nutrients to plants more uniformly (Rotz et al., 2005). In addition, as the plant litter inputs, mesofaunal feeding rate and root turnover rate were greater in un-grazed and rabbit than fully grazed grassland more nutrients may be returned to the soil via decomposition in these grazing regimes.

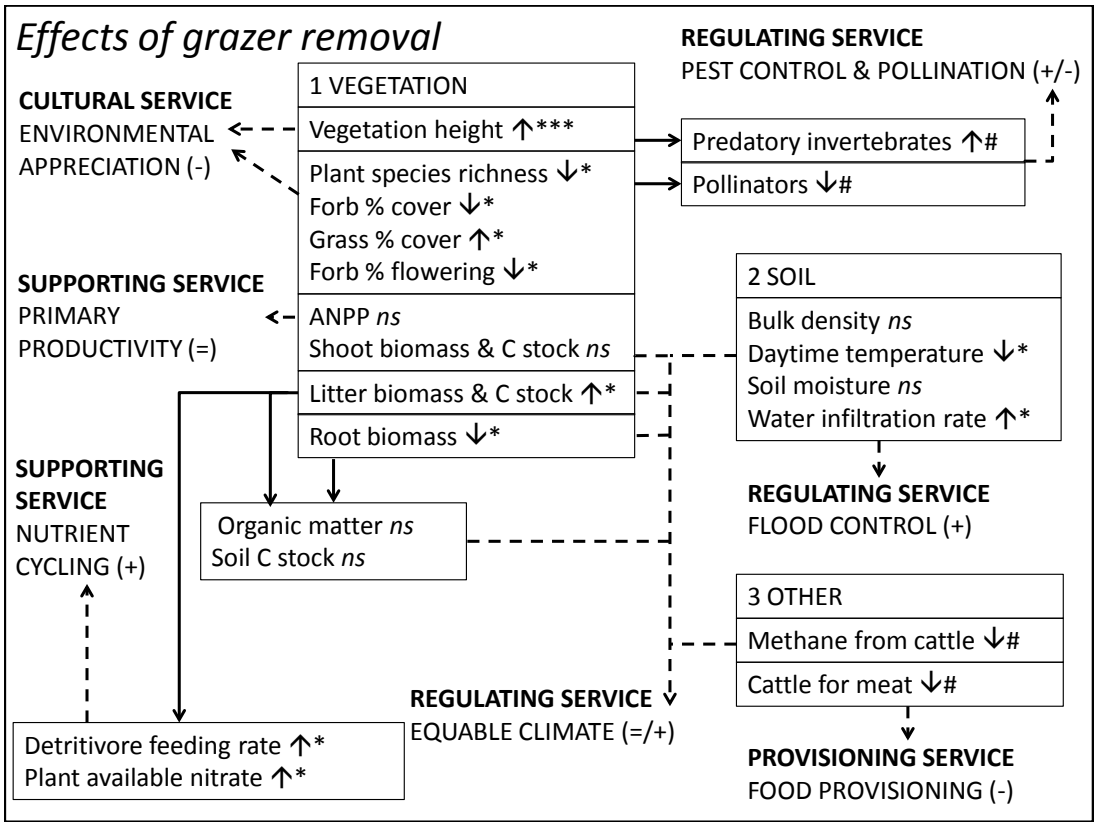

Figure 3.6 Effects of pony and cattle removal from coastal grassland on measured variables and potential ecosystem service delivery. Significant increase or decrease in variables indicated by up (↑) or down (↓) arrows (*p < 0.05, ***p < 0.001, *ns* = not significant), # for expected results from the literature. Direct links between variables (solid lines), indirect links to ecosystem services (dashed lines) with positive (+), equal (=) or negative (-) effects on ecosystem services are also shown.

3.5.2 Provisioning services

It can be argued that the low intensity grazed coastal grassland is more important than other grassland management types for the provisioning service of food supply, with good quality beef or lamb produced at low stocking levels (Wood et al., 2007). This service would be lost upon removal of grazing. However, as grazing abandonment is not a static state, with natural succession shrubs and trees will dominate and non-commercial food sources such as nuts and berries may become important to some people, but these benefits are difficult to quantify (Everard et al., 2010). Genetic diversity of wild species may be enhanced by the use of rare breeds of cattle for conservation grazing and seed from semi-natural grassland used to create species-rich grasslands under agri-environmental schemes (Bullock et al., 2011). This service may be enhanced by extensive grazing management to maximise plant biodiversity.

Fresh drinking water supply, via recharge of aquifers under grassland is another key provisioning service. This service is also provided by both chalk aquifers underlying semi-natural grasslands and vast swathes of UK upland grasslands that are major water catchments (Holland et al., 2011; Koo and O'Connell, 2006). In this study water infiltration rates increased when large herbivores were removed, regardless of the presence or absence of rabbits, as large grazers are responsible for soil compaction (Elliott and Carlson, 2004). Even though the study coastal grassland is largely level, in sloping habitats it is likely that high water infiltration rates will improve water storage and reduce run-off (Marshall et al., 2009). It may therefore be proposed that rabbit grazed or un-grazed grasslands should be promoted on hillsides where water storage is important for land managers. If primary succession continues in the un-grazed or 'abandoned' grassland, shrubs are likely to dominate and the pattern of water infiltration and water storage may be reversed, with greater water storage in the grazed grassland due to lower evapo-transpiration rates (Chartier et al., 2011).

3.5.3 Regulating services

Regulating services include maintenance of an equable climate, control of flooding and water quality and pest regulation and pollination. Semi-natural grasslands play an important part in maintenance of an equable climate as they are a valuable C store, according to current evidence emit little nitrous oxide and have lower methane emissions than intensively managed grasslands due to lower stocking levels (Bullock et al., 2011; Jones and Donnelly, 2004; Soussana et al., 2004). There is currently little consensus on the role of grazing in grassland C sequestration. Light, moderate or heavy grazing can all increase soil C, depending on grassland type (Kemp and Michalk, 2007). Conversely extensive grazing or no grazing may also increase C storage (Campbell et al., 1997; Soussana et al., 2004) and lead to increased C storage. This study found that total C stock from four combined pools, soil, roots, litter and shoots, did not differ with grazing intensity but that root C was greatest in fully and rabbit grazed, while litter C was greatest in rabbit and un-grazed grassland. As root-derived C contributed more to total C stock than litter or shoot-derived C and root-derived C has a residence time of 2.5 times that of litter or shoot derived C (Rasse et al., 2005) there is potential for greater C storage in the grazed grassland.

Water storage within grassland groundwater also maintains regulating functions such as moderating overland flow, reducing flooding and improving water quality by reducing nutrients and pathogenic bacteria than often contaminate surface waters (Bullock et al., 2011; Kemp and Michalk, 2007). The decreased infiltration rates due to compaction caused by grazing of cattle or other large herbivores leads to higher runoff and N contamination via faeces or urine (Cheng-Zhang and Squires, 2010; Rotz et al., 2005). By contrast, grazing abandonment increases infiltration rates with significant potential as a tool to manage flood risk (Carroll et al., 2004).

Invertebrate abundance and diversity, particularly of large predatory spiders, carabids and staphylinids is often higher in un-grazed grasslands (Ford et al., 2012a; Morris, 2000), with potential implications for pest regulation where semi-natural grasslands border arable fields. Our results show the opposite, with greatest

abundance and diversity of predatory invertebrates in the fully grazed grassland. As catch size was consistently greatest in fully grazed, intermediate in rabbit grazed and smallest in un-grazed it is likely that increased structural complexity of vegetation in the rabbit grazed and un-grazed treatments resulted in reduction of catch (Melbourne, 1999), therefore these results may not capture true abundance and diversity of predatory invertebrates. Nectar feeders and therefore pollinators, including bumble bees, hoverflies and butterflies, tend to be driven by floral abundance, floral richness, availability of nectar resources and sward structure (Potts et al., 2003; Sjödin et al., 2008), all factors influenced by grazing intensity. Grazing also affects soil microbial diversity, with clear effects on microbial composition in both sand dunes and saltmarsh (Ford et al., 2012b), although the implications for ecosystem services provision are unclear.

3.5.4 Cultural services

Proof of the importance of coastal grasslands to cultural services includes the conservation status of coastal grasslands as a UK Biodiversity Action Plan (UK BAP) listed priority habitat with some important plants, nationally scarce invertebrates (Alexander et al., 2005), birds such as RDB3 skylarks (*Alauda arvensis*) and BAP listed priority amphibian, natterjack toad (*Epidalea calamita*). Environmental appreciation and recreation are also key cultural services in semi-natural grasslands and coastal sand dunes in particular attract significant numbers of tourists (Bullock et al., 2011; Jones et al., 2011). Aesthetic appreciation of the environment is likely to improve with reduction in grass in favour of increased abundance of flowering plants (Mitteager et al., 2006; Paar et al., 2008). In this study plant species richness, particularly for forbs, and flower abundance were significantly greater in fully than in un-grazed habitat. Tall grasses were more dominant in the un-grazed areas, indeed *Arrhenatherum elatius,* a negative indicator species of fixed dune grassland, was present only within rabbit grazed and un-grazed grassland. Plassmann et al. (2010) also found that the number of positive indicator species was lower in un-grazed grassland. Therefore a tentative conclusion could be drawn that aesthetic appreciation is greater in extensively grazed than un-grazed grassland.

3.5.5 Grazing management for conservation

Mixed grazing is often recommended as grazing with both horses and cattle can lead to enhanced control of competitive grass species, opening up gaps for other plant species and increases in structural diversity compared to cattle grazing alone (Loucougaray, 2004). Welsh mountain ponies graze on poor quality forage and avoid flowering heads, with potential positive results for plant diversity, flowering and aesthetics, as argued in this study. Sheep will graze a sward shorter than either cattle or ponies and may select high quality plant parts such as flowers, pods and young shoots (Rook et al., 2004), making them less suitable for conservation grazing. Despite the majority of north–west European grassland managers promoting low intensity grazing by ponies and/or cattle, Newton et al. (2009), in a systematic review of grazing management, found that the presence of grazers consistently lead to a decline in 'tussocky' vegetation with negative effects on reptile and invertebrate habitat. Rotational grazing, where animals are moved at regular time intervals allowing vegetation time to 'recover', often has favourable effects on plant, bird and invertebrate diversity (Söderström et al., 2001; Wrage et al., 2011). It is also recognised that un-grazed vegetative buffer zones adjacent to riparian or arable fields, can allow spatial co-delivery of multiple ecological services, although these are rarely quantified (Olson & Wäckers, 2007). Where large grazers are removed rabbit grazing may define habitat characteristics, keeping patches of grassland fairly open, with a lower mean sward height than un-grazed grassland, preventing major declines in plant or forb diversity but allowing soil to become less compact (Isermann et al., 2010) with greater infiltration rates, results mirrored by this study. However, rabbits are often dependent on large herbivores to maintain the short vegetation they prefer, and these effects may not persist.

3.5.6 Ecosystem service tradeoffs

In the light of abandonment of low productivity grazing land throughout Europe, in addition to biodiversity measures of 'success' in conservation, ecosystem service measures and trade-offs need to be taken into account when choosing an appropriate grassland management scheme. Results from this case study and the

wider scientific literature indicate that extensively cattle grazed or mixed pony/cattle grazed grassland should be conserved for the ecosystem services of plant genetic diversity, food provision, cultural environmental appreciation and potential pollination services. Un-grazed grassland should be conserved for the ecosystem services of invertebrate biodiversity, water storage and flood control (particularly on hill-side slopes), nutrient cycling and the potential for pest regulation. Rabbit grazed grasslands provide slightly lower plant biodiversity and cultural services than grazed grasslands but similar water infiltration dynamics to un-grazed grasslands. Grazing management should depend on the conservation objectives for a particular habitat but should take into account likely trade-offs with other ecosystem services. Perhaps grassland managers, whilst maintaining extensively grazed areas, could trial the introduction of rabbit grazed or un-grazed 'buffer strips' next to water courses, natural boundaries or arable fields, to minimise biodiversity and ecosystem service trade-offs.

3.6 Acknowledgements

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3.8 Appendix

Table A3.1 Invertebrate species counts for all grazing treatments from pitfalls and pan traps (nectar feeders only); COL (Coleoptera), ARA (Araneae), HYM (Hymenoptera), HET (Heteroptera), CHI (Chilopoda), HET (Heteroptera), OPI (Opiliones), DIC (Dictyoptera), ORT (Orthoptera), PUL (Pulmonata), ISO (Isopoda), DIP (Diploda), DER (Dermaptera), HAP (Haplotaxida); sorted by functional group; PRE (Predatory), ZOO (Zoophagous), OMN (Omnivore), PHY (Phytophagous, (B) Bryophyte feeder), POL (Pollen feeder), DET (Detritivore, (F) Fungivorous, (S) Scavenging), MYR (Myrmecophilous), DUN (Dung feeder), NEC (Nectar feeders) NOT (Not assigned). Spiders; FRH (foliage running hunter), GRH (ground running hunter), SA (Stalker/Ambusher), SWB (Space web builder), OW (Orb weaver), SW (Sheet weaver). N (nationally scarce), RDB3 (Red data book 3 listed), * (associated with coastal dune habitat; Alexander et al., 2005).

Order	Family	Species	Common name	Group	PR	R	U	Total
COL	Staphylinidae	*Tachyporus atriceps*	Rove beetle	PRE[1]	24	10	2	36
COL	Staphylinidae	*Tachyporus dispar*	Rove beetle	PRE[1]	6	3	0	9
COL	Staphylinidae	*Tachinus marginellus*	Rove beetle	PRE[1]	0	0	1	1
COL	Staphylinidae	*Amischa analis*	Rove beetle	PRE[1]	1	1	1	3
COL	Staphylinidae	*Oxypoda lentula*	Rove beetle	PRE[1]	1	0	0	1
COL	Staphylinidae	*Othius subuliformis*	Rove beetle	PRE[1]	2	1	0	3
COL	Staphylinidae	*Quedius boops*	Rove beetle	PRE[1]	2	0	0	2
COL	Staphylinidae	*Quedius curtipennis*	Rove beetle	PRE[1]	3	0	0	3
COL	Staphylinidae	*Quedius fuliginosus*	Rove beetle	PRE[1]	1	2	0	3
COL	Staphylinidae	*Quedius semiobscurus*	Rove beetle	PRE[1]	6	4	0	10
COL	Staphylinidae	*Quedius molochinus*	Rove beetle	PRE[1]	1	0	2	3
COL	Staphylinidae	*Quedius levicollis*	Rove beetle	PRE[1]	1	3	0	4
COL	Staphylinidae	*Philonthus carbonarius*	Rove beetle	PRE[1]	1	0	0	1
COL	Staphylinidae	*Philonthus cognatus*	Rove beetle	PRE[1]	1	0	0	1
COL	Staphylinidae	*Philonthus splendens*	Rove beetle	PRE[1]	0	1	0	1
COL	Staphylinidae	*Philonthus varians*	Rove beetle	PRE[1]	1	0	0	1
COL	Staphylinidae	*Ocypus aenocephalus*	Rove beetle	PRE[1]	13	5	0	18
COL	Staphylinidae	*Ocypus brunnipes*	Rove beetle	PRE[1]	3	2	3	8
COL	Staphylinidae	*Ocypus olens*	Rove beetle	PRE[1]	1	0	0	1
COL	Staphylinidae	*Stenus clavicornis*	Rove beetle	PRE[1]	2	2	6	10
COL	Staphylinidae	*Stenus ossium*	Rove beetle	PRE[1]	0	1	1	2
COL	Staphylinidae	*Stenus pusillus*	Rove beetle	PRE[1]	1	0	0	1
COL	Staphylinidae	*Stenus juno*	Rove beetle	PRE[1]	5	2	1	8
COL	Staphylinidae	*Stenus latifrons*	Rove beetle	PRE[1]	0	1	0	1
COL	Staphylinidae	*Stenus nigritulus*	Rove beetle	PRE[1]	1	0	0	1
COL	Staphylinidae	*Xantholinus linearis*	Rove beetle	PRE[1]	6	4	0	10
COL	Staphylinidae	*Xantholinus longiventris*	Rove beetle	PRE[1]	2	1	1	4
COL	Staphylinidae	*Aleochara sparsa*	Rove beetle	PRE[1]	0	1	0	1
COL	Cantharidae	*Rhagonycha fulva*	Soldier beetle	PRE[2]	10	0	0	10
COL	Coccinellidae	*Rhyzobius litura*	Lady bird	PRE[2]	5	2	1	8
COL	Coccinellidae	*Nephus redtenbacheri*	Lady bird	PRE[2]	1	2	1	4
COL	Coccinellidae	*Subcoccinella vigintiquattuorpunctata*	Lady bird	PRE[2]	3	1	2	6
COL	Histeridae	*Kissiter minimus*	Water beetle	PRE[3]	1	0	0	1
COL	Carabidae	*Nebria salina*	Ground beetle	ZOO[4]	1	0	0	1
COL	Carabidae	*Dyschirius globosa*	Ground beetle	ZOO[4]	2	0	1	3

COL	Carabidae	*Pterostichus versicolor*	Ground beetle	ZOO[4]	1	0	0	1
COL	Carabidae	*Calathus fuscipes*	Ground beetle	ZOO[4]	24	7	0	31
COL	Carabidae	*Calathus melanocephalus*	Ground beetle	ZOO[4]	23	8	0	31
COL	Carabidae	*Badister bipustulatus*	Ground beetle	ZOO[4]	8	5	5	18
COL	Carabidae	*Metabletus foveatus*	Ground beetle	ZOO[4]	2	1	0	3
COL	Carabidae	*Notiophilus aquaticus*	Ground beetle	ZOO[4]	1	0	0	1
COL	Carabidae	*Trechus obtusus*	Ground beetle	ZOO[4]	0	0	1	1
COL	Carabidae	*Pterostichus niger*	Ground beetle	ZOO[4]	0	2	0	2
COL	Carabidae	*Amara aenea*	Ground beetle	PHY[4]	4	3	0	7
COL	Carabidae	*Amara communis*	Ground beetle	PHY[4]	0	4	0	4
COL	Carabidae	*Amara lucida*	Ground beetle	PHY[4] N	1	3	0	4
COL	Carabidae	*Amara lunicollis*	Ground beetle	PHY[4]	2	4	3	9
COL	Carabidae	*Amara ovata*	Ground beetle	PHY[4]	0	0	1	1
COL	Carabidae	*Amara tibialis*	Ground beetle	PHY[4]	3	1	0	4
COL	Carabidae	*Harpalus tardus*	Ground beetle	PHY[4]	2	1	1	4
COL	Leiodidae	*Leiodes rugosa*	Fungus beetle	PHY[5]	2	0	0	2
COL	Leiodidae	*Leiodes rufipennis*	Fungus beetle	PHY[5]	12	10	2	24
COL	Leiodidae	*Sciodrepoides watsoni*	Fungus beetle	PHY[5]	1	0	0	1
COL	Leiodidae	*Catops fuliginosus*	Fungus beetle	PHY[5]	0	0	8	8
COL	Leiodidae	*Catops morio*	Fungus beetle	PHY[5]	0	2	2	4
COL	Leiodidae	*Agathidium laevigatum*	Fungus beetle	PHY[5]	1	0	0	1
COL	Byrrhidae	*Simplocaria semistriata*	Pill beetle	PHY[5] (B)	0	2	0	2
COL	Dryopidae	*Dryops ernesti*	Long-toed water beetle	PHY[5]	2	0	0	2
COL	Dryopidae	*Dryops luridus*	Long-toed water beetle	PHY[5]	0	0	1	1
COL	Tenebrionidae	*Lagria hirta*	Darkling beetle	PHY[5]	2	0	2	4
COL	Tenebrionidae	*Melanimon tibialis*	Darkling beetle	PHY[5]	7	5	1	13
COL	Tenebrionidae	*Phylan gibbus*	Darkling beetle	PHY[5]	2	2	1	5
COL	Tenebrionidae	*Cteniopus suphureus*	Darkling beetle	PHY[5]	1	1	0	2
COL	Chrysomelidae	*Chrysomela populi*	Leaf beetle	PHY[5]	2	0	0	2
COL	Chrysomelidae	*Galerucella tenella*	Leaf beetle	PHY[5]	1	0	0	1
COL	Chrysomelidae	*Lochmaea capreae*	Leaf beetle	PHY[5]	1	3	0	4
COL	Chrysomelidae	*Longitarsus gracilis*	Leaf beetle	PHY[5]	1	2	0	3
COL	Chrysomelidae	*Longitarsus luridus*	Leaf beetle	PHY[5]	6	5	0	11
COL	Chrysomelidae	*Longitarsus jacobaea*	Leaf beetle	PHY[5]	39	1	0	40
COL	Chrysomelidae	*Cassida prasina*	Leaf beetle	PHY[5]	0	0	1	1
COL	Chrysomelidae	*Chaetocnema hortensis*	Leaf beetle	PHY[5]	1	0	0	1
COL	Chrysomelidae	*Neocrepidodera ferruginea*	Leaf beetle	PHY[5]	20	13	1	34
COL	Chrysomelidae	*Neocrepidodera transversa*	Leaf beetle	PHY[5]	1	0	0	1
COL	Curculionidae	*Otiorrhynchus ovatus*	Weevil	PHY[5]	1	2	1	4
COL	Curculionidae	*Philopedon plagiatus*	Weevil	PHY[5]	10	12	4	26
COL	Curculionidae	*Sitona lineellus*	Weevil	PHY[5]	3	1	0	4
COL	Curculionidae	*Hypera plantaginis*	Weevil	PHY[5]	7	3	0	10
COL	Curculionidae	*Apion pubescens*	Weevil	PHY[5]	3	0	0	3
COL	Elateridae	*Agrypnus murinus*	Click beetle	POL[6]	33	20	3	56
COL	Elateridae	*Agriotes obscurus*	Click beetle	POL[6]	11	5	0	16
COL	Hydrophilidae	*Megasternum concinnum*	Water beetle	DET[7]	19	10	6	35
COL	Staphylinidae	*Anotylus tetracarinatus*	Rove beetle	DET[1]	1	0	0	1
COL	Staphylinidae	*Ischnosoma splendidum*	Rove beetle	DET[1] (F)	0	1	5	6
COL	Staphylinidae	*Mycetoporus piceolus*	Rove beetle	DET[1] (F) N	5	9	13	27
COL	Staphylinidae	*Mycetoporus punctus*	Rove beetle	DET[1] (F) N	0	1	0	1
COL	Staphylinidae	*Atheta brunneipennis*	Rove beetle	DET[1] (F)	0	0	1	1
COL	Staphylinidae	*Micropeplus staphylinoides*	Rove beetle	DET[1] (F)	0	1	0	1
COL	Latridiidae	*Corticaria minuta*	Scavenger beetle	DET[8] (F)	0	0	1	1
COL	Staphylinidae	*Drusilla caniculatata*	Rove beetle	MYR[1]	0	6	0	6
COL	Staphylinidae	*Zyras collaris*	Rove beetle	MYR[1]	0	0	1	1
COL	Staphylinidae	*Platydracus stercorarius*	Rove beetle	MYR[1]	9	6	0	15
COL	Scarabaeidae	*Aphodius prodromus*	Dung beetle	DUN[9]	0	1	0	1
COL	Scarabaeidae	*Onthophagus similis*	Dung beetle	DUN[9]	5	0	1	6
COL	Scarabaeidae	*Geotrupes stercorarius*	Dung beetle	DUN[9]	0	0	2	2
COL	Scarabaeidae	*Aphodius fimetarius*	Dung beetle	DUN[9]	1	0	0	1
COL	Scarabaeidae	*Aphodius rufipes*	Dung beetle	DUN[9]	1	0	0	1

COL	Scarabaeidae	*Sericea brunnea*	Dung beetle	DUN[9]	0	1	0	1
COL	Carabidae	*Philorhizus melanocephalus*	Ground beetle	NOT	0	1	2	3
COL	Staphylinidae	*Mocyta fungi*	Rove beetle	NOT	23	13	12	48
COL	Staphylinidae	*Pella limbata*	Rove beetle	NOT	0	0	1	1
COL	Staphylinidae	*Bisnius sordidus*	Rove beetle	NOT	4	0	0	4
COL	Staphylinidae	*Badura macrocera*	Rove beetle	NOT	1	0	0	1
COL	Staphylinidae	*Megalinus glabratus*	Rove beetle	NOT	3	0	0	3
COL	Lampyridae	*Lampyris noctiluca*	Glow worm	NOT	3	1	1	5
ARA	Clubionidae	*Cheiracanthium virescens*	Foliage spider	PRE[10] (FRH)	1	0	0	1
ARA	Clubionidae	clubionid juveniles	Foliage spider	PRE[10] (FRH)	3	1	0	4
ARA	Gnaphosidae	*Drassodes cupreus*	Ground spider	PRE[10] (GRH)	10	3	2	15
ARA	Gnaphosidae	*Haplodrassus signifer*	Ground spider	PRE[10] (GRH)	0	2	0	2
ARA	Gnaphosidae	*Zelotes electus*	Ground spider	PRE[10] (GRH)	19	6	0	25
ARA	Gnaphosidae	*Zelotes latreillei*	Ground spider	PRE[10] (GRH)	4	19	16	39
ARA	Gnaphosidae	*Micraria pulicaria*	Ground spider	PRE[10] (GRH)	0	0	1	1
ARA	Gnaphosidae	Gnaphosid juveniles	Ground spider	PRE[10] (GRH)	2	12	1	15
ARA	Lycosidae	*Pardosa monticola*	Wolf spider	PRE[10] (GRH)	643	371	5	1019
ARA	Lycosidae	*Pardosa palustris*	Wolf spider	PRE[10] (GRH)	33	2	0	35
ARA	Lycosidae	*Pardosa armentata*	Wolf spider	PRE[10] (GRH)	2	0	0	2
ARA	Lycosidae	*Pardosa pullata*	Wolf spider	PRE[10] (GRH)	103	360	269	732
ARA	Lycosidae	*Pardosa nigriceps*	Wolf spider	PRE[10] (GRH)	15	52	145	212
ARA	Lycosidae	*Alopeosa barbipes*	Wolf spider	PRE[10] (GRH)	1	0	0	1
ARA	Lycosidae	*Alopecosa pulverulenta*	Wolf spider	PRE[10] (GRH)	49	27	7	83
ARA	Lycosidae	*Trochosa ruricola*	Wolf spider	PRE[10] (GRH)	1	0	0	1
ARA	Lycosidae	*Trochosa terricola*	Wolf spider	PRE[10] (GRH)	10	6	2	18
ARA	Lycosidae	lycosid juveniles	Wolf spider	PRE[10] (GRH)	122	98	44	264
ARA	Thomisidae	*Xysticus cristatus*	Crab spider	PRE[10] (SA)	11	2	0	13
ARA	Thomisidae	*Xysticus erraticus*	Crab spider	PRE[10] (SA)	17	4	0	21
ARA	Thomisidae	*Xysticus kochi*	Crab spider	PRE[10] (SA)	11	1	0	12
ARA	Thomisidae	*Ozyptila atomaria*	Crab spider	PRE[10] (SA)	1	0	0	1
ARA	Thomisidae	*thomisid juveniles*	Crab spider	PRE[10] (SA)	9	3	2	14
ARA	Salticidae	*Euophys frontalis*	Jumping spider	PRE[10] (SA)	0	0	1	1
ARA	Salticidae	*Heliophanus flavipes*	Jumping spider	PRE[10] (SA)	0	0	1	1
ARA	Theridiidae	*Enoplognatha thoracica*	Comb spider	PRE[10] (SWB)	1	0	0	1
ARA	Dictynidae	*Argenna subnigra*	Mesh webbed spider	PRE[10] (SWB)	58	60	4	122
ARA	Tetragnathidae	*Pachygnatha degeeri*	Orb weaver	PRE[10] (OW)	473	212	25	710
ARA	Linyphiidae	*Ceratinella brevipes*	Sheet weaver	PRE[10] (SW)	1	0	0	1
ARA	Linyphiidae	*Ceratinella brevis*	Sheet weaver	PRE[10] (SW)	0	0	2	2
ARA	Linyphiidae	*Walckenaeria acuminata*	Sheet weaver	PRE[10] (SW)	0	2	9	11
ARA	Linyphiidae	*Walckenaeria antica*	Sheet weaver	PRE[10] (SW)	11	14	6	31
ARA	Linyphiidae	*Walckenaeria atrotibialis*	Sheet weaver	PRE[10] (SW)	0	3	1	4
ARA	Linyphiidae	*Walckenaeria monoceros*	Sheet weaver	PRE[10] (SW)	18	2	1	21
ARA	Linyphiidae	*Walckenaeria vigilax*	Sheet weaver	PRE[10] (SW)	0	1	0	1
ARA	Linyphiidae	*Dicymbium nigrum*	Sheet weaver	PRE[10] (SW)	8	3	0	11
ARA	Linyphiidae	*Peponocranium ludicrum*	Sheet weaver	PRE[10] (SW)	0	0	1	1
ARA	Linyphiidae	*Oedothorax fuscus*	Sheet weaver	PRE[10] (SW)	4	0	1	5
ARA	Linyphiidae	*Oedothorax retusus*	Sheet weaver	PRE[10] (SW)	5	0	0	5

ARA	Linyphiidae	*Pelecopsis parallela*	Sheet weaver	PRE[10] (SW)	2	0	0	2
ARA	Linyphiidae	*Pocadicnemis pumila*	Sheet weaver	PRE[10] (SW)	1	0	3	4
ARA	Linyphiidae	*Mecopisthes peusi*	Sheet weaver	PRE[10] (SW) N	13	3	1	17
ARA	Linyphiidae	*Trichopterna thorelli*	Sheet weaver	PRE[10] (SW)	0	2	0	2
ARA	Linyphiidae	*Cnephalocotes obscurus*	Sheet weaver	PRE[10] (SW)	0	2	1	3
ARA	Linyphiidae	*Erigone atra*	Sheet weaver	PRE[10] (SW)	5	0	0	5
ARA	Linyphiidae	*Erigone dentipalpis*	Sheet weaver	PRE[10] (SW)	3	0	0	3
ARA	Linyphiidae	*Tiso vagans*	Sheet weaver	PRE[10] (SW)	95	69	12	176
ARA	Linyphiidae	*Troxochrus scabriculus*	Sheet weaver	PRE[10] (SW)	0	1	3	4
ARA	Linyphiidae	*Tapinocyba praecox*	Sheet weaver	PRE[10] (SW)	11	0	2	13
ARA	Linyphiidae	*Gongylidiellum vivum*	Sheet weaver	PRE[10] (SW)	15	9	6	30
ARA	Linyphiidae	*Erigonella hiemalis*	Sheet weaver	PRE[10] (SW)	0	1	0	1
ARA	Linyphiidae	*Agyneta decora*	Sheet weaver	PRE[10] (SW)	5	1	1	7
ARA	Linyphiidae	*Centromerita concinna*	Sheet weaver	PRE[10] (SW)	3	6	0	9
ARA	Linyphiidae	*Centromerus prudens*	Sheet weaver	PRE[10] (SW)	0	0	1	1
ARA	Linyphiidae	*Stemonyphantes lineatus*	Sheet weaver	PRE[10] (SW)	2	1	0	3
ARA	Linyphiidae	*Bathyphantes gracilis*	Sheet weaver	PRE[10] (SW)	3	2	0	5
ARA	Linyphiidae	*Bathyphantes parvulus*	Sheet weaver	PRE[10] (SW)	4	1	0	5
ARA	Linyphiidae	*Lepthyphantes tenuis*	Sheet weaver	PRE[10] (SW)	23	10	2	35
ARA	Linyphiidae	*Lepthyphantes mengei*	Sheet weaver	PRE[10] (SW)	0	6	1	7
ARA	Linyphiidae	*Lepthyphantes pallidus*	Sheet weaver	PRE[10] (SW)	6	23	5	34
ARA	Linyphiidae	*Lepthyphantes zimmermani*	Sheet weaver	PRE[10] (SW)	1	2	0	3
ARA	Linyphiidae	*juveniles Linyphiidae**	Sheet weaver	PRE[10] (SW)	55	33	6	94
HYM	Formicidae	*Lasius fuliginosus*	Ant	PRE[11] (P)	0	0	1	1
HYM	Formicidae	*Lasius mixtus*	Ant	PRE[12] (P)	3	8	9	20
HYM	Formicidae	*Lasius umbratus*	Ant	PRE[13] (P)	1	0	0	1
HET	Nabidae	*Nabis flavomarginatus*	Damsel bug	PRE[14]	0	1	0	1
CHI	Lithobiidae	*Lithobius microps*	Centipede	PRE[15]	0	1	2	3
HET	Dipsocoridae	*Ceratocombus coleoptratus*		PRE[16]	0	0	8	8
OPI	Nemastomatidae	*Nemastoma bimaculata*	Harvestmen	ZOO[15]	0	0	1	1
OPI	Phalangiinae	*Lacinius ephippiatus*	Harvestmen	ZOO[15]	0	5	2	7
OPI	Phalangiinae	*Platybunus triangularis*	Harvestmen	ZOO[15]	5	7	2	14
OPI	Phalangiinae	*Lophopilio palpinalis*	Harvestmen	ZOO[15]	0	3	0	3
OPI	Phalangiinae	*Oligolophus tridens*	Harvestmen	ZOO[15]	1	0	0	1
OPI	Phalangiinae	*Phalangium opilio*	Harvestmen	ZOO[15]	204	53	4	261
OPI	Phalangiinae	*Opilio saxatilis*	Harvestmen	ZOO[15]	20	22	10	52
OPI	Leiobunidae	*Leiobunum blackwalli*	Harvestmen	ZOO[15]	0	0	1	1
OPI	Leiobunidae	*Leiobunum rotundum*	Harvestmen	ZOO[15]	0	1	0	1
OPI		*immature harvesters**	Harvestmen	ZOO[15]	36	23	20	79
HYM	Formicidae	*Formica fusca*	Ant	OMN[2]	3	2	2	7
HYM	Formicidae	*Lasius niger*	Ant	OMN[17]	36	47	77	160
HYM	Formicidae	*Myrmica rubra*	Ant	OMN[2]	1	30	10	41
HYM	Formicidae	*Myrmica ruginodis*	Ant	OMN[17]	9	34	23	66
HYM	Formicidae	*Myrmica sabuleti*	Ant	OMN[17]	165	124	4	293
HYM	Formicidae	*Myrmica scabrinodis*	Ant	OMN[17]	21	10	34	65
DIC	Ectobiinae	*Ectobius panzeri*	Cockroach	OMN[18]	11	2	1	14
HET	Tingidae	*Acalypta parvula*	Lace bug	PHY[14]	71	34	38	143
HET	Berytidae	*Berytinus minor*	Stilt bug	PHY[14]	4	3	0	7
HET	Berytidae	*Berytinus montivagus*	Stilt bug	PHY[14]	3	2	0	5
HET	Tingidae	*Kalama tricornis*	Lace bug	PHY[14]	204	110	9	323
HET	Lygaeidae	*Megalonotus praetextatus*	Ground bug	PHY[14] N	0	1	0	1
HET	Lygaeidae	*Stygnocoris sabulosus*	Ground bug	PHY[14]	2	0	1	3
HET	Lygaeidae	*Plinthiscus brevipennis*	Ground bug	PHY[14]	0	0	1	1
HET	Rhopalidae	*Myrmus miriformis*		PHY[14]	0	1	1	2
ORT	Acrididae	*Chorthippus brunneus*	Grasshopper	PHY[15] *	0	0	1	1
ORT	Acrididae	*Omocestus viridulus*	Grasshopper	PHY[15] *	0	2	0	2
ORT	Acrididae	*Myrmeleotettix maculatus*	Grasshopper	PHY[15] *	1	1	0	2
PUL			Snails & slugs	PHY[15]	150	153	80	383
ISO	Trichoniscidae	*Trichoniscus pusillus*	Woodlouse	DET[15] (S)	0	1	0	1
ISO	Philosciidae	*Philoscia muscorum*	Woodlouse	DET[15] (S)	295	1251	136	1682
ISO	Armadillidiidae	*Armadillidium vulgare*	Woodlouse	DET[15] (S)	52	347	37	436
ISO	Porcellionidae	*Porcellio scaber*	Woodlouse	DET[15] (S)	71	123	116	310
DIP	Julidae	*Cylindroiulus latestriatus*	Millipede	DET[15] (S)	354	196	137	687
DIP	Julidae	*Julus scandinavius*	Millipede	DET[15] (S)	0	0	1	1
DIP	Julidae	*Ophyiulus pilosus*	Millipede	DET[15] (S)	20	1	3	24
DIP	Julidae	*Brachyiulus pusillus*	Millipede	DET[15] (S)	15	7	8	30

DIP	Julidae	*Omatoiulus sabulosus*	Millipede	DET[15] (S)	0	1	0	1
DIP	Polydesmidae	*Polydesmus angustatus*	Millipede	DET[15] (S)	2	3	1	6
DER	Forficulidae	*Forficula auricularia*	Earwig	DET[15] (S) *	14	4	1	19
HAP	Lumbricidae.		Earthworm	DET[15] NEC[2]	53	30	11	94
HYM	Colletidae	*Colletes cunicularius*	Mining bee	RDB3	0	0	2	2
HYM	Colletidae	*Colletes fodiens*	Solitary bee	NEC[2]	1	0	0	1
HYM	Andrenidae	*Andrena nigroaenea*	Mining bee	NEC[2]	0	0	1	1
HYM	Halictidae	*Lasioglossum albipes*	Solitary bee	NEC[2]	4	2	1	7
HYM	Megachilidae	*Osmia aurulenta*	Mason bee	NEC[2]	0	0	4	4
HYM	Megachilidae	*Osmia rufa*	Red mason bee	NEC[2]	0	0	1	1
HYM	Colletidae	*Hylaeus communis*	Yellow face bee	NEC[2]	2	4	3	9
HYM	Apinae	*Bombus hortorum*	Bumble bee	NEC[2]	3	6	0	9
HYM	Apinae	*Bombus lapidarius*	Bumble bee	NEC[2]	0	5	13	18
HYM	Apinae	*Bombus pascuorum*	Bumble bee	NEC[2]	5	4	6	15
HYM	Apinae	*Bombus terrestris*	Bumble bee	NEC[2]	0	7	0	7
HYM	Apinae	*Bombus bohemicus*	Bumble bee	NEC[2]	3	0	0	3
HYM	Apinae	*Bombus lucorum*	Bumble bee	NEC[2]	0	0	11	11
HYM	Apidae	*Apis mellifera*	Honey bee	NEC[2]	0	0	5	5

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Chapter 4: Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure

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4.1 Abstract

1. Saltmarsh conservation management often involves livestock grazing to maximise plant diversity and provide suitable breeding habitat for over-wintering coastal birds. The effect of grazing on invertebrates is rarely quantified, but results from limited studies of terrestrial and coastal grasslands demonstrate greater abundance and species richness in un-grazed grassland.

2. The impact of short sward (< 8 cm) cattle grazing on the ground dwelling invertebrate community was assessed on an English inter-tidal upper salt marsh using pitfall traps. Abundance, species richness, functional group structure, abundance of coastal specialists, environmental factors that influence invertebrate habitat choice and food web composition were compared for grazed and un-grazed marsh.

3. In total, 90000 invertebrates were sampled. Predatory, zoophagus and detritivorous Coleoptera were significantly more abundant on the un-grazed marsh. In contrast, predatory Hemiptera and Araneae were significantly more abundant on the grazed marsh. Sheet weaver spiders were significantly more abundant on the grazed marsh, foliage running hunters and space web builders more abundant on the un-grazed marsh. Most inter-tidal coastal specialist species exhibited clear habitat preference for the grazed marsh. Total species richness was not significantly different between grazing treatments.

4. RDA analysis showed that two environmental variables influenced by grazing intensity, soil temperature and vegetation height, significantly explained the composition of invertebrate functional groups. Larger bodied invertebrates dominated the un-grazed food web.

5. We conclude that both short sward cattle grazed and un-grazed saltmarsh habitat should be maintained to maximise invertebrate abundance and diversity and provide suitable habitat for coastal specialists.

Key words Araneae, biodiversity, body size, Coleoptera, Hemiptera, food web, insects, pitfall, prey capture method, spiders.

4.2 Introduction

European salt marshes are highly productive and were traditionally managed as agricultural livestock grazing land (Bouchard *et al.*, 2003; Doody, 2008). Grazing is still common place within the salt marshes of North West Europe and is often maintained with the twin conservation aims of maximising plant and bird diversity (Chatters, 2004; Milsom *et al*., 2000). It is well known that intermediate grazing pressure maximises plant diversity on Northern European marshes (Adam, 1990; Bakker *et al*., 1993). Birds, however, show a variable response to grazing intensity as each species exhibits a particular habitat preference (Daan *et al.*, 2002; Bouchard *et al.*, 2003). Salt marshes are also an important coastal habitat for both highly specialised inter-tidal invertebrates (Pétillon *et al.*, 2005), certain Red Data Book (RDB) listed or Biodiversity Action Plan (BAP) species (Alexander *et al*., 2005; Webb *et al.*, 2010) and other invertebrates common to grasslands.

The effects of saltmarsh grazing management on invertebrate diversity and abundance are poorly understood. Previous saltmarsh invertebrate studies have tended to focus on the zonation of particular groups, especially carabid beetles and spiders, with marsh elevation. Irmler *et al.* (2002) and Finch *et al.* (2007) both found that species richness of carabid beetles and Araneae increased with distance above mean high tide. British carabid and Staphylinidae saltmarsh communities have also been well documented (Hammond, 2000; Luff & Eyre, 2000). Most studies report

higher invertebrate species richness and abundance in un-grazed systems for both salt marshes and other grasslands (Bakker *et al.*, 1993; Gibson *et al.*, 1992a; Morris, 2000; Kruess & Tscharntke, 2002). Pétillon *et al.* (2007) found that although this was true for spiders, for Coleoptera species richness was higher on grazed marsh. Short sward, livestock grazed marshes provide a suitable habitat for inter-tidal coastal specialist species (Andresen *et al.*, 1990).

We define invertebrate coastal specialists as those species that are only found in inter-tidal or estuarine habitats. These species are habitually or physiologically adapted to cope with tidal inundation and variable salinity. Some species, such as the saltmarsh spider *Pardosa purbeckensis* avoid flooding by moving vertically in tall vegetation, but if submerged in saline water they survive longer than related terrestrial wolf spiders (Pétillon *et al.,* 2011). Another saltmarsh spider, *Arctosa fulvolineata*, withstands submersion by entering a hypoxic coma (Pétillon *et al.,* 2009). Some invertebrate species can osmoregulate in saline environments, controlling the water balance within their bodies (Williams & Hamm, 2002). Other marine invertebrates take advantage of plastron respiration (Flynn & Bush, 2008). Terrestrial invertebrates that occur in habitats likely to flood are often opportunists able to migrate horizontally to higher ground, enter a dormant stage underwater or reproduce rapidly to take advantage of flood free periods (Adis & Junk, 2002).

Livestock grazing reduces above-ground biomass and vegetation height, causes a rapid turnover of plant material via the production of fresh leaves, reduces plant litter build up and has direct effects on plant species composition and structure via preference or avoidance of particular plant species by livestock (Adam, 1990; Bos, 2002). Sheep provide a uniform short sward whereas cattle, as more selective feeders, often produce a more 'tussocky' sward (Adam, 1990; Lambert, 2000). With high stocking density cattle can however produce a short, even sward of high quality forage, attractive for feeding geese, or provide variable structure, suitable for breeding birds (Bakker, 1989; Bos, 2002). In contrast, either in historically un-grazed or abandoned upper salt marshes tall unpalatable grasses, such as *Elytrigia athericus* dominate (Bakker *et al*., 1993; Van Wijnen & Bakker, 1997; Bakker *et al*., 2002). Livestock grazing also impacts upon abiotic marsh characteristics. Short

grazed vegetation leads to greater and more variable soil temperatures than un-grazed grassland (Curry, 1994). Cattle disturbance generally results in a topographically variable soil surface whereas sheep evenly compact it, but both can lead to waterlogged ground with high soil salinity (Lambert, 2000). Grazing herbivores also return nutrients to the soil via dung input (Bakker *et al*., 1993).

Abundance and diversity of terrestrial invertebrate fauna is greatest on un-grazed marshes, with a food web dominated by detritivores, as tall vegetation and increased litter layer depth increase available niches, food provision and provide cover from predators (Adam, 1990; Curry, 1994). The grazed marsh invertebrate food web is dominated by warmth seeking inter-tidal coastal specialists and phytophagus individuals dependent upon particular plant species (Andresen *et al.*, 1990; Bakker *et al.*, 1993). If grazing intensity is very high phytophagus invertebrates also decline (Meyer *et al.,* 1995). The marsh invertebrate food web can be characterised using functional groups (Blondel, 2003), in our study different trophic categories. 'Bottom-up' processes such as resource limitation or 'top-down' processes such as population limitation by predators can be studied using a functional group approach (Chen & Wise, 1999). Few studies have looked at the response of saltmarsh invertebrate functional groups to grazing. Meyer *et al*. (1995) described how the European saltmarsh invertebrate food web differed with sheep grazing intensity but most studies focus on either the macro-invertebrate community of the lower marsh (Salgado *et al*., 2007) or American saltmarsh food webs (Zimmer *et al*. 2004). As the marshes of North America differ from European marshes in terms of productivity, dominant plant species, effect of livestock grazing upon plant species richness and invertebrate community (Bazely & Jeffries, 1986; Adam, 1990; Ford & Grace, 1998; Garbutt & Boorman, 2009), it is difficult to relate North American food web studies to European marshes.

Coleoptera communities are affected by moisture, temperature, salinity, vegetation height, trampling and soil compaction (Lassau *et al.*, 2005; Pétillon *et al.*, 2008; Hofmann & Mason, 2006; Morris, 2000). Spider species assemblages are particularly sensitive to moisture, vegetation height and vegetation structure (Bonte *et al.*, 2000; Uetz *et al.*, 1999; Bell *et al.*, 2001; Pétillon *et al.*, 2008). In a

Californian saltmarsh a positive relationship was found between plant species richness, vegetation tip height diversity and spider family richness due to increased potential of nesting and web building sites (Traut, 2005). Hemiptera, phytophagus Auchenorrhyncha leafhoppers in particular, increase in abundance and diversity with greater plant diversity, vegetation height and structural complexity (Biedermann *et al*., 2005). *E. atherica* invasion of salt marshes, characteristic of un-grazed marshes, correlates to an increase in non coastal spider species leading to an overall increase in biodiversity but a decrease in abundance of coastal specialist species (Pétillon *et al.*, 2005; Pétillon *et al.*, 2010). Spider coastal specialists may decline as *E. atherica* stands tend to create drier more terrestrial conditions than other saltmarsh vegetation. Un-grazed inland salt meadows also exhibited a lower abundance of coastal specialist spider species than grazed meadows (Zulka *et al*., 1997).

The existing evidence suggests that un-grazed marshes may provide suitable habitat for a diverse invertebrate community, but that cattle grazed marshes with a uniform short sward may support a narrower range of saltmarsh specialist species. Prey selection within food webs may be influenced by body size of invertebrates; however, no published work has been carried out relating saltmarsh food web structure to body size of invertebrates. This study aims to assess the impact of grazing on abundance, diversity and functional group structure of the entire ground dwelling invertebrate community using pitfall sampling. Specifically addressing how grazing influences: abundance, species richness and functional group structure of Coleoptera, Hemiptera and Araneae; abundance and functional group structure of all other invertebrates; abundance of invertebrate coastal specialists; environmental factors that influence invertebrate habitat choice; and saltmarsh food web in relation to functional group and body size. The three main orders focused on within this study, Coleoptera, Hemiptera and Araneae, were chosen as they are well studied, easy to identify to species level, include important predators, often include larger bodied individuals and are used as bio-indicators of grassland ecosystem health (Biedermann *et al*., 2005; Pearce & Venier, 2006).

4.3 Methods

4.3.1 Site description

The salt marshes of the Ribble estuary cover around 2000 ha in total. The study area, Crossens Marsh (53^{o} 41' 15" N, 2^{o} 57' 4" W), is located on the southern edge of the Ribble estuary in North-West England and is part of the Sefton Coast Special Protection Area managed by Natural England, the statutory conservation body. The marsh was historically un-grazed but was split into two management types over 40 years ago, un-grazed and cattle grazed (Figure 4.1). The grazed marsh is characterised by predominantly *Festuca rubra* saltmarsh NVC community (SM16d) and the un-grazed marsh by *Elytrigia repens* saltmarsh (SM28; Rodwell, 2000). *E. repens* replaces *E. atherica* on UK west coast. The grazed part of the marsh covers 517 ha and is uniformly grazed by around 100 bullocks from late May to early October, approximately 0.2 cattle per hectare, and provides a consistent short sward (< 8 cm) for overwintering pink-footed geese (*Anser brachyrhynchus*) to feed. Small herbivores such as field voles are also present, particularly on the un-grazed marsh.

Figure 4.1 Crossens Marsh field site with fence line marking boundary between un-grazed vegetation on the left, dominated by a tall sward (20 – 30 cm) of *Elytrigia repens*, and consistently short cattle grazed vegetation on the right (< 8 cm).

4.3.2 Experimental design

All experimental units were selected within the high marsh zone where numerous creeks are present but tidal inundations are relatively rare, limited to around eight events a year on high equinox tides. A paired experimental design was used with six experimental units of approximately 10 m x 10 m set up on each side of a 600 m long section of the fence line, 100-150 m apart, in a 'mirror image' formation, giving six grazed (G1-G6) and six un-grazed (U1-U6) units (Figure 4.2). Each experimental unit was located between 20 m and 50 m from the fence line to ensure an adequate buffer zone and checked for standard elevation within ±10 cm. All measurements were carried out within these experimental units.

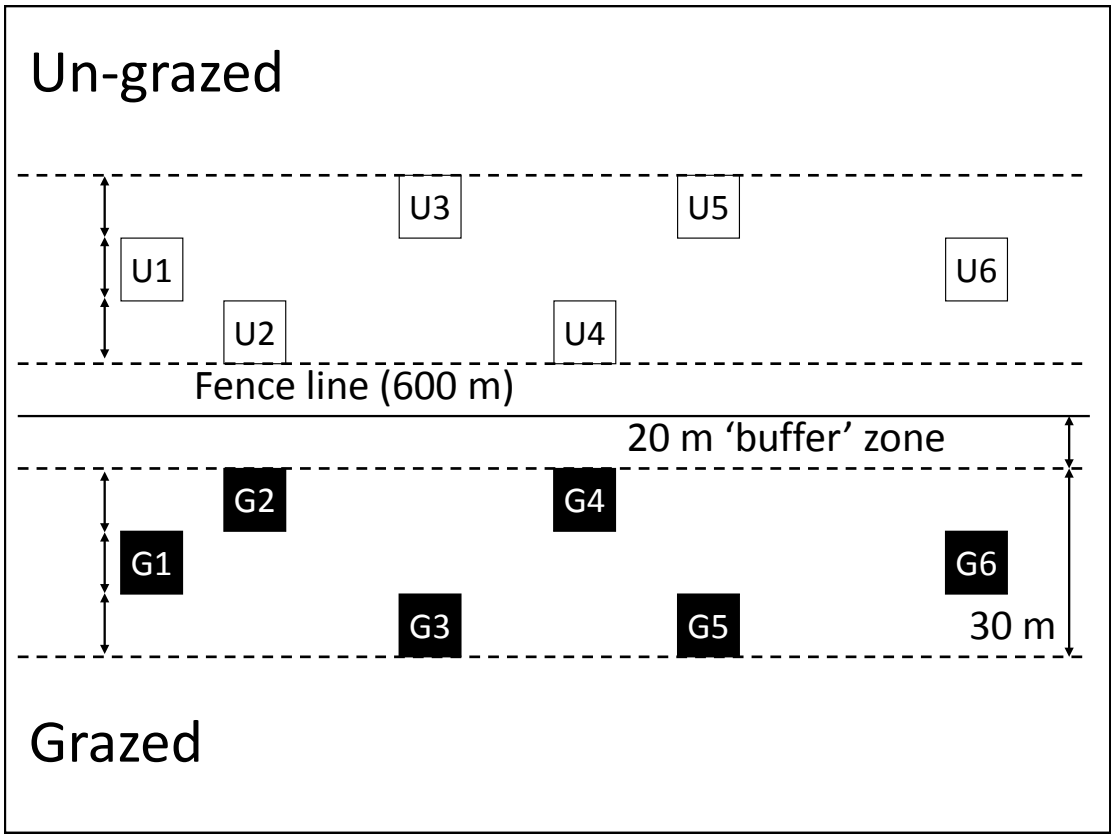

Figure 4.2 Experimental design at Crossens Marsh, G1–G6 were grazed experimental units, U1-U6 were un-grazed units.

4.3.3 Soil and vegetation characteristics

Soil samples were collected during September 2009 from the top 15 cm of soil to measure salinity and pH. Soil was sieved to 2 mm and a sub sample of 10 g was

taken from each sample and shaken with 25 ml of deionised water (1:2.5 dilution factor). A *Hanna* pH209 pH meter was used to measure pH and a *Jenway* 4520 Conductivity meter to measure electrical conductivity (mS cm^{-1}) as a proxy for salinity (Douaik, Van Meirvenne & Tóth, 2007). Samples to determine bulk density and soil organic matter content were collected during September 2009 using intact soil cores of 3.8 cm diameter and 15 cm depth. Cores were dried at 105 ^{o}C for 72 hours and the dry mass divided by the volume of the core to calculate bulk density. Loss-on-ignition was used to estimate organic matter content (Ball, 1964). Soil moisture content and temperature were recorded at six locations within each experimental unit during September. Soil conductivity was measured in direct volts using a *Delta T* Theta Meter HH1 (four probes of 6 cm) and converted to percentage soil moisture content using a calibration suitable for organic soils. Soil temperature was measured using a digital thermometer (single 11 cm probe).

Plant species richness and percentage cover were estimated by eye during July 2009 in five 1 m x 1 m quadrats placed 3 m apart within each experimental unit. Within each quadrat a 25 cm x 50 cm corner was allocated and above-ground living vegetation collected. Plant litter was collected separately from the same area. One root core of 5 cm diameter and 10 cm depth was also taken per quadrat and washed to remove all soil. Above-ground vegetation, litter and roots were all dried at 80 °C for 24 hours and weighed to give indicators of above-ground live plant biomass, litter biomass and below-ground root biomass respectively. Vegetation height was measured in May and September at ten random positions within 1 m of each pitfall trap with a custom made drop disc of 20 cm diameter, 10 g mass. Vegetation height diversity was also calculated. All plant nomenclature follows Stace (2010).

4.3.4 Ground dwelling invertebrates - pitfall traps

Pitfall traps were used to sample ground dwelling invertebrates in spring and autumn. The traps were put in place for 28 days from 5th May to 2nd June 2009 and for 30 days between 4th September and 9th October 2009 (excluding 5 days where traps were removed due to high tides). Six pitfall traps per experimental unit were

set up in two lines of three, 5 m apart. Each trap consisted of a plastic cup (80 mm diameter x 105 mm deep) a third full with a 50/50 mix of ethylene glycol and water, recommended for preservation of invertebrates (Schmidt *et al*., 2006), with a drop of washing up liquid to break the surface tension. Each trap was pushed into a hole made by a soil auger until they were flush with the soil surface. A rain hat was placed over each trap and set at 3 cm from the ground. A wire basket of 5 cm mesh size was also placed over each rain hat and pegged down to prevent interference by cattle. Pitfalls were emptied and replaced with new ethylene glycol mixture half way through the spring and autumn sampling periods to aid preservation of invertebrates. The contents of the pitfalls were preserved in 70 % Industrial strength methylated spirits (IMS).

4.3.5 Invertebrate classification - functional groups & coastal specialists

All invertebrates caught in the pitfall traps from Coleoptera, Hemiptera and Araneae were identified to species level, all other invertebrates were identified to family or order level. All invertebrates were also classified according to the following functional groups: predatory, zoophagus (predatory and scavenging), phytophagus (herbivore or granivorous), detritivore (feed on detritus and associated decomposer community of fungi and bacteria) (Kreeger & Newell, 2000), or an additional category 'not assigned' on the basis of species, family or order level information (Table A4.1). Invertebrate species authorities listed in Table A4.1. Spiderlings were excluded from the analysis as they were only counted in September. Larvae belonging to all other groups were assigned a functional group where possible. Araneae are all predators but were further grouped by prey capture method as proposed by Uetz *et al.* (1999).

Coastal specialist carabid beetles were defined by Luff (1998), Araneae by Harvey *et al.* (2002). Nationally scarce invertebrates associated with coastal saltmarsh were defined by Buglife – The Invertebrate Conservation Trust (Alexander *et al.* 2005), these species are not necessarily coastal specialists but are nationally scarce invertebrates only found in particular habitats. The UK distribution of coastal specialist species were also checked using the National Biodiversity Network

interactive map (http://data.nbn.org.uk/imt, 2011). Invertebrate nomenclature follows Duff (2008) for Coleoptera and Fauna Europea (2004) for Araneae, Hemiptera and all other groups.

4.3.6 Statistical Analysis – soil and vegetation characteristics

Differences between grazing treatments for soil and vegetation characteristics were analysed using linear mixed effects models (lme) analysed by ANOVA using R v.2.12.1 (2010 As lme (salinity ~ grazing, random = ~1|block/grazing). This approach was used to enable the raw data to be analysed accounting for replication at the level of the experimental unit or block (n=6). Vegetation height diversity for the grazed and un-grazed marsh was calculated from the Coefficent of variance (CoV; Standard Deviation/Mean*100) of each set of ten heights from around each pitfall.

4.3.7 Statistical Analysis – ground dwelling invertebrates

For each of the twelve experimental units, the contents of the six pitfalls within each unit were pooled to give a total invertebrate count per unit. As trends in invertebrate community composition appeared similar between the May and September sampling periods the data were combined to give one measure of abundance to represent the year 2009. At the level of the experimental unit (n=6) differences in functional group abundance and species richness, within Coleoptera, Hemiptera, Araneae and all other invertebrate groups, between grazed and un-grazed treatments were tested for statistical significance using Wilcoxon matched pairs test, Genstat v.10 (Payne *et al.*, 2007). Box plots were produced using Minitab v.15 Statistical Software (2007).

4.3.8 Statistical Analysis – relationship between environmental variables and functional group occurrence

Linear direct gradient analysis (RDA) was carried out to examine the relationship between all environmental variables listed in Table 4.1 (mean at unit level), and the distribution of pitfall functional groups and prey capture methods from the six grazed and six un-grazed experimental units of the salt marsh. 'Species' data were entered into the analysis in the form log transformed count data (total for

experimental unit) of functional groups or Araneae prey capture methods, RDA scaling was focused on inter-species correlations and centred by species, grazing treatment of each unit was included in the final RDA triplot but was not used to influence the analysis. The significance of environmental variables was tested using automatic forward selection (Monte Carlo test, 500 permutations). All multivariate analysis was carried out in Canoco v.4.5 (Ter Braak and Šmilauer, 2003).

4.3.9 Food web analysis

The most abundant groups of invertebrates on the grazed or un-grazed marsh (≥ 1% of total abundance on one marsh type) were used to create a food web for the salt marsh based on taxonomy, functional group, body size and prey selection preferences. Body size was divided into three size classes based on body length, large (≤ 30 mm), medium (≤ 20 mm) and small (≤ 10 mm). Body size was determined for Coleoptera (Unwin, 1988), Hemiptera (Burrows, 2009; Bantock & Botting, 2010), Araneae (Jones-Walters, 1989) and other invertebrates (Chinery, 1986; Tilling, 1987). Food web prey preferences, both for particular invertebrate groups and body size, were based on Lövei & Sunderland (1996), Clough *et al*. (2007), Rickers (2005) and Landis & Werf (1997) for predatory beetles and Hemiptera; Nyffeler (1999), Jones-Walters (1989) and Enders (1975) for spiders; Dias & Hassal (2005) for woodlice and sand hoppers.

4.4 Results

4.4.1 Soil properties and vegetation characteristics

Soil bulk density, percentage moisture content and temperature were all significantly higher on the grazed marsh; soil pH was significantly higher on the un-grazed marsh (Table 4.1). Plant species richness; percentage cover of *Agrostis stolonifera*, *Glaux maritima*, *Puccinellia maritima* and *Triglochin maritima*; and below-ground plant biomass were all significantly greater on the grazed marsh. Percentage cover of *Elytrigia repens*, above-ground plant biomass, litter biomass, vegetation height in May and September were all significantly higher on the un-grazed marsh. Soil salinity, soil organic matter content, percentage cover of *Festuca*

rubra and vegetation height diversity were not significantly different between grazing treatments.

4.4.2 Invertebrate summary

This study captured nearly 90,000 ground dwelling invertebrates, around two thirds on the un-grazed marsh. Predators were one and a half times more abundant on the grazed than the un-grazed marsh, but not significantly so, 19 % and 9 % respectively of the total invertebrate count per grazing treatment. Zoophagus invertebrates were three times more abundant on the un-grazed marsh (Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$) and phytophagus individuals were equal between treatments, both groups only accounted for 1 - 3 % of total count per treatment. There were twice as many detritivores on the un-grazed than the grazed marsh, 78 % compared to 55 % of the total. There were twice as many not assigned invertebrates on the grazed marsh, 23 % to 9 % on the un-grazed. Coleoptera accounted for 6 %, Hemiptera 1 % and Araneae 9% of the total invertebrate count. For Coleoptera, Hemiptera and Araneae combined species richness was not significantly different between grazing treatments.

4.4.3 Abundance, species richness and functional group structure of Coleoptera

Coleoptera were around three times more abundant and significantly more species rich (Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$, Table 4.2) on the un-grazed marsh. Predatory, Zoophagus and Detritivorous Coleoptera were all significantly more abundant on the un-grazed marsh (Test statistics for each: Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$; Figure 4.3a). The most abundant species on the un-grazed marsh were zoophagus *Bembidion iricolor* (14 % of total Coleoptera), predatory *Cantharis rufa* (14 %) and predatory *Cordalia obscura* (11 %). The most abundant species on the grazed marsh were zoophagus *Bembidion aeneum (20 %)*, not assigned *Brundia marina* (14 %) and *C. rufa* (14 %).

Table 4.1 Soil properties and vegetation characteristics measured from the grazed and un-grazed marsh. Sampling depths are presented alongside treatment means ± standard errors, ANOVA results (n = 6), number of replicate samples per experimental unit and month sampled. For vegetation height, for each of the 6 replicates per treatment the mean of 10 measurements was used in the analysis. For vegetation height diversity, CoV = coefficient of variance.

	Depth (cm)	Grazed	Un-grazed		Reps	Month
Soil						
Salinity (mS cm^{-1})	0-15	4.2 ± 0.4	3.4 ± 0.3	*ns*	3	Sept.
pH	0-15	7.6 ± 0.1	7.9 ± 0.1	*	3	Sept.
Bulk density (g cm^{-3})	0-15	0.8 ± 0.0	0.7 ± 0.0	*	3	Sept.
Organic matter content (%)	0-15	7.4 ± 0.7	6.3 ± 0.4	*ns*	3	Sept.
Moisture content (%)	0-6	52.6 ± 0.1	44.5 ± 1.2	*	6	Sept.
Temperature (^{o}C)	0-11	14.9 ± 0.1	14.2 ± 0.0	*	6	Sept.
Vegetation						
Plant species richness (species m^{-2})	n/a	6.6 ± 0.3	3.7 ± 0.2	*	5	July
% cover						
Agrostis stolonifera L.	n/a	20.0 ± 5.3	0.0 ± 0.0	*	5	July
Elytrigia repens L.	n/a	0.7 ± 0.5	58.0 ± 6.0	**	5	July
Festuca rubra L.	n/a	25.4 ± 4.7	31.2 ± 5.4	*ns*	5	July
Glaux maritima L.	n/a	6.0 ± 1.4	0.0 ± 0.0	**	5	July
Puccinellia maritima Parl.	n/a	28.3 ± 5.7	0.0 ± 0.0	*	5	July
Triglochin maritima L.	n/a	11.3 ± 2.4	3.2 ± 2.8	*	5	July
Above ground biomass (kg dwt m^{-2})	n/a	0.3 ± 0.0	0.7 ± 0.1	*	5	July
Litter biomass (kg dwt m^{-2})	n/a	0.0 ± 0.0	0.3 ± 0.0	*	5	July
Below ground biomass (kg dwt m^{-2})	0-10	3.4 ± 0.2	1.0 ± 0.1	***	5	July
Vegetation height (cm)	n/a	8.1 ± 0.5	29.2 ± 0.8	***	6	May
Vegetation height (cm)	n/a	8.2 ± 0.4	19.2 ± 0.7	***	6	Sept.
Vegetation height diversity (CoV) (%)	n/a	31.5 ± 4.6	29.9 ± 3.2	*ns*	6	May
Vegetation height diversity (CoV) (%)	n/a	29.1 ± 3.7	32.6 ± 3.8	*ns*	6	Sept.

Significant differences between grazing treatments indicated by *($p < 0.05$), **($p < 0.01$) and ***($p < 0.001$). Non significant results recorded as *ns* ($p > 0.05$).

4.4.4 Abundance, species richness and functional group structure of Hemiptera

Hemiptera were around five times more abundant on the grazed than the un-grazed marsh but total species richness did not differ (Table 4.2). Predatory Hemiptera were significantly more abundant on the grazed marsh (Wilcoxon; $w = 0$, $p < 0.05$, Figure 4.3b), phytophagus Hemiptera did not differ with grazing. On the grazed marsh the predatory shore bug *Salda littoralis* accounted for 67 % of total Hemipteran abundance. Phytophagus aphids accounted for 18 % of total abundance on the grazed marsh, 61 % on the un-grazed marsh.

Table 4.2 Invertebrate species richness comparison between grazed and un-grazed marsh; Coleoptera, Hemiptera and Araneae combined, separated into orders and at a functional group or prey capture method level. Species richness data are shown by treatment medians ± inter-quartile range, n = 6 in all cases.

Invertebrate group	Functional group / prey capture method	Grazed	Un-grazed	
Coleoptera, Hemiptera, Araneae	All	51.0 ± 6.8	60.5 ± 7.3	*ns*
Coleoptera	All	28.0 ± 6.5	37.0 ± 1.5	*
Coleoptera	Predatory	10.0 ± 3.5	13.0 ± 1.5	*ns*
Coleoptera	Zoophagus	8.0 ± 0.8	9.0 ± 0.8	*ns*
Coleoptera	Phytophagus	5.0 ± 1.5	5.0 ± 1.5	*ns*
Coleoptera	Detritivore	3.0 ± 0.8	7.0 ± 2.8	*ns*
Coleoptera	Not assigned	2.0 ± 0.0	2.0 ± 0.0	*ns*
Hemiptera	All	6.0 ± 1.5	5.5 ± 2.5	*ns*
Hemiptera	Predatory	2.0 ± 0.0	1.0 ± 0.8	*ns*
Hemiptera	Phytophagus	4.5 ± 1.8	4.0 ± 1.5	*ns*
Araneae	All / Predatory	17.5 ± 1.8	20.0 ± 2.3	*ns*
Araneae	Foliage running hunter	0.5 ± 0.0	1.0 ± 0.0	*ns*
Araneae	Ground running hunter	4.5 ± 1.0	6.0 ± 0.8	*ns*
Araneae	Space web builder	0.0 ± 0.0	1.0 ± 0.0	*
Araneae	Sheet weavers	12.7 ± 0.5	12.0 ± 0.8	*ns*

Significant differences between grazing treatments indicated by *($p < 0.05$), non significant results as *ns* ($p > 0.05$), Wilcoxon Matched-Pairs test.

4.4.5 Abundance, species richness and prey capture methods of Araneae

As an entirely predatory group Araneae were significantly more abundant on the grazed marsh (Wilcoxon; w = 0, d.f. = 5, $p < 0.05$, Figure 4.4a) but species richness did not differ (Table 4.2). Foliage running hunters were significantly more abundant on the un-grazed marsh (Wilcoxon; w = 0, d.f. = 5, $p < 0.05$, Figure 4.4b). Ground running hunter abundance was not significantly different between the grazed and un-grazed marsh. Space web builders were more abundant on the un-grazed marsh (Wilcoxon; w = 0, d.f. = 5, $p < 0.05$). Sheet weavers were significantly more abundant (Wilcoxon; w = 0, d.f. = 5, $p < 0.05$) but not more species rich on the grazed marsh. The grazed marsh was numerically dominated by two sheet weaver Linyphiidae species, *Erigone longipalpis* (42 % of total Araneae for grazing treatment) and *Oedothorax fuscus* (21 %). The wolf spider *P. purbeckensis* (9 %) were also common on the grazed marsh. The un-grazed marsh was characterised by the Linyphiidae *Allomengea scopigera* (39 %) and *P. purbeckensis* (20 %).

4.4.6 Abundance and functional group structure of other invertebrates

For all other invertebrates total abundance was twice as high on the un-grazed marsh. Zoophagus invertebrates, all harvestmen, were significantly more abundant on the un-grazed marsh (Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$, Figure 4.5a). Predatory (all parasitoid wasps), phytophagus, detritivore and not assigned functional groups did not differ significantly with grazing treatment (Figure 4.5a, 4.5b). Even though the abundance of all detritivores did not differ between grazing treatments their composition did. On the un-grazed marsh *Orchestia gammerella* (68 %) and woodlice (23 %) were most abundant. On the grazed marsh Collembola (69 %) and *O. gamerella* (30 %) were common. Of particular interest within the not assigned category are the Tipulidae, these were caught fifty times more frequently on the grazed marsh.

4.4.7 Abundance of coastal specialist species

Coastal specialist ground beetles, *Bembidion minimum* and *Dicheirotrichus gustavii*, rove beetle *B. marina* and nationally scarce saltmarsh shore bug *Saluda opacula* were found predominantly on the grazed side of the marsh (Table A4.1). As were Araneae coastal specialist species *Silometopus ambiguus* and *E. longipalpis.* The coastal spider *P. purbeckensis* was found almost equally on both the grazed and the un-grazed marsh. The carabid *B. iricolor* was recorded mainly on the un-grazed side. Even though *D. gustavii* and *S. opacula* show clear habitat preferences they are only found in low numbers compared to the other coastal specialist species listed. Three species, *B. marina*, *S. ambiguus* and *E. longipalpis* were sampled in greater abundances in G5, the most saline experimental unit, than any of the other units.

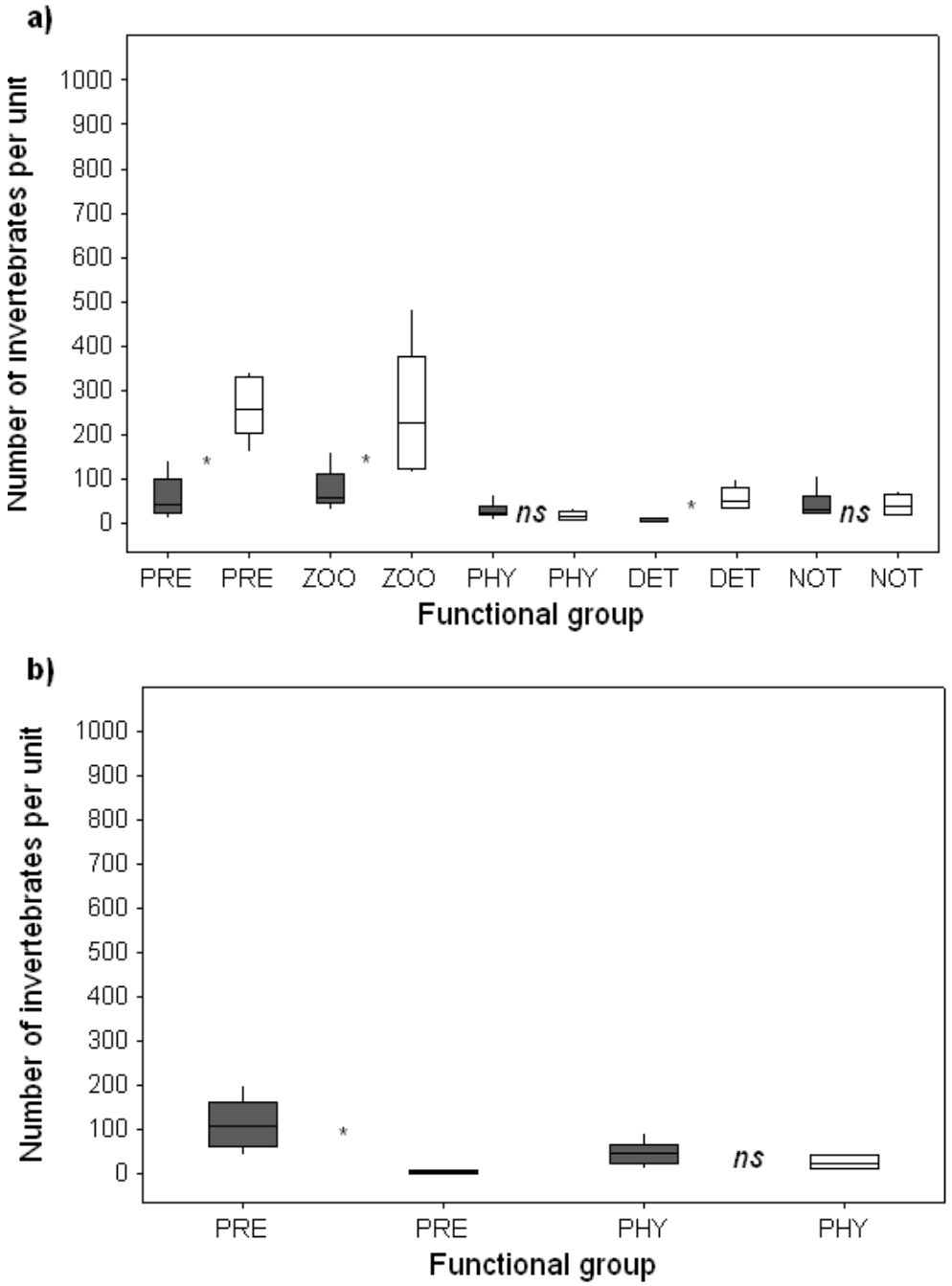

Figure 4.3 Coleoptera (a) and Hemiptera (b) abundance from grazed (grey bars) and un-grazed (white bars) salt marsh characterised by functional group: PRE = predatory; ZOO = zoophagus; PHY = phytophagus; DET = detritivore; NOT = not assigned. Significant differences between grazing treatment indicated by *($p < 0.05$), non significant results as *ns* ($p > 0.05$), Wilcoxon matched pairs test.

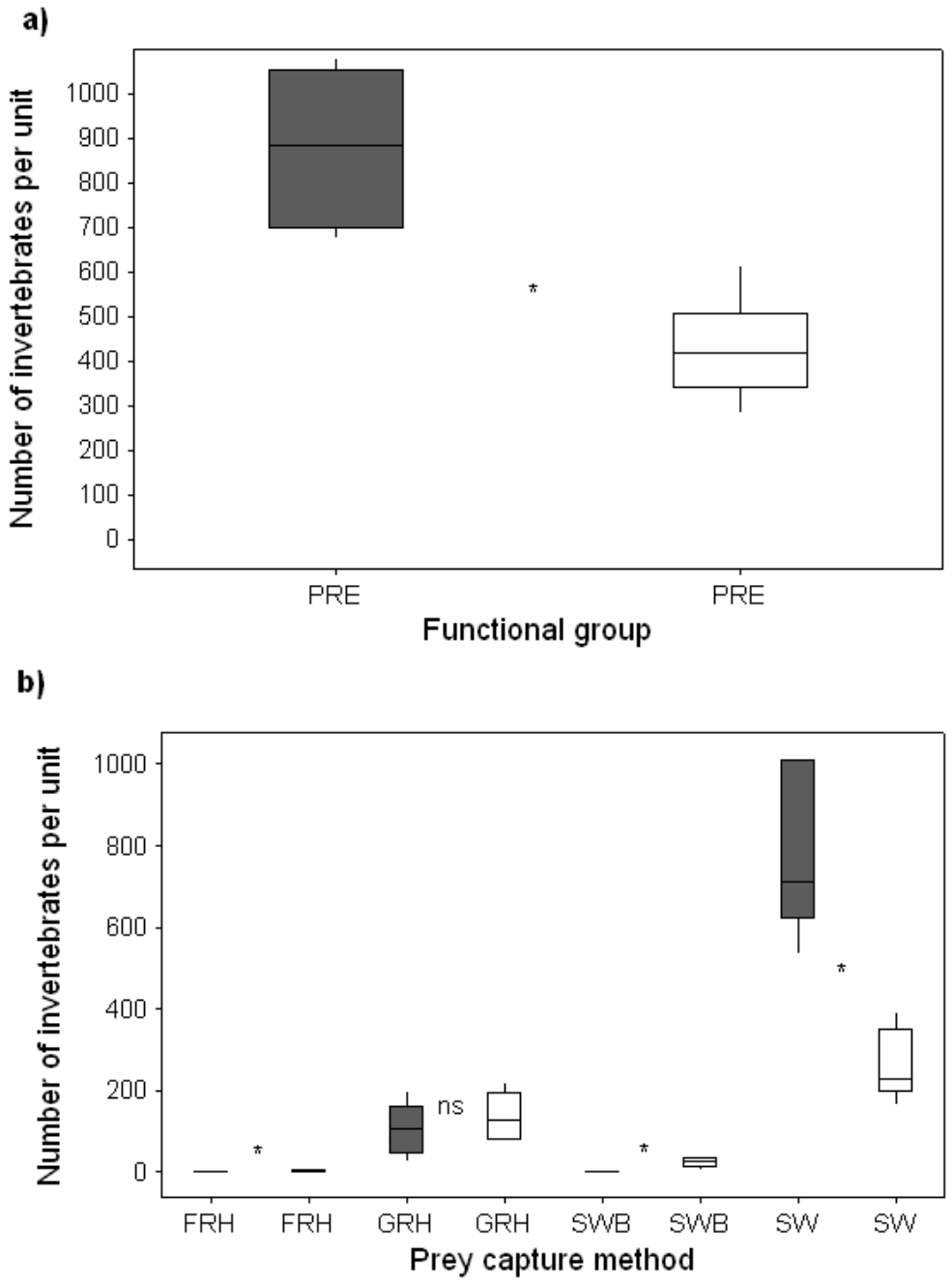

Figure 4.4 Araneae abundance from grazed (grey bars) and un-grazed (white bars) salt marsh characterised by functional group (a): PRE = predatory and further classified by prey capture method (b): FRH = foliage running hunter; GRH = ground running hunter; SWB = space web builder; SW = sheet weaver. Significant differences between grazing treatment indicated by *($p < 0.05$), non significant results as *ns* ($p > 0.05$), Wilcoxon matched pairs test.

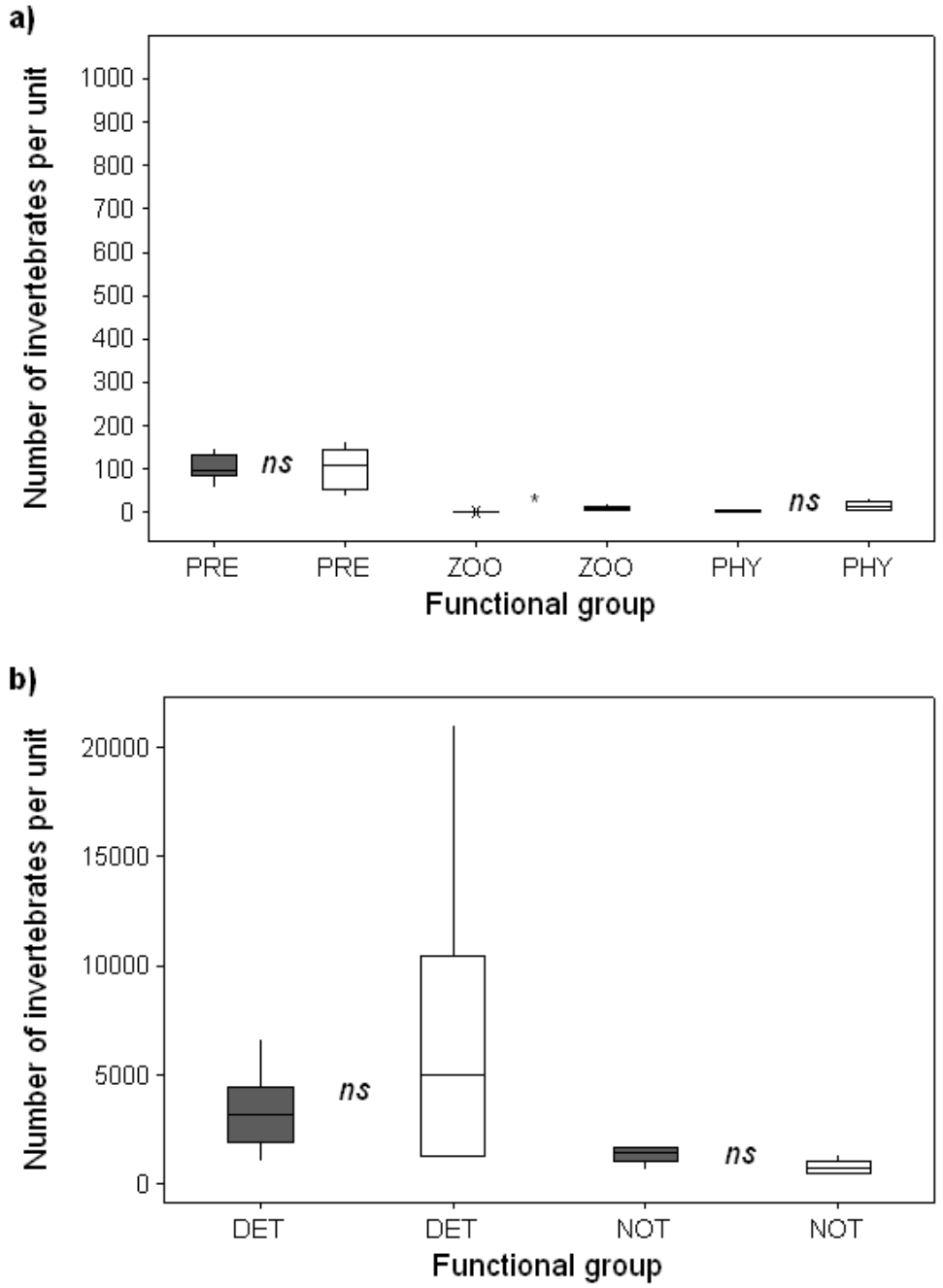

Figure 4.5 All other invertebrates (not Coleoptera, Hemiptera or Araneae) abundance from grazed (grey bars) and un-grazed (white bars) salt marsh characterised by functional group: a) PRE = predatory; ZOO = zoophagus & PHY = phytophagus; b) DET = detritivore & NOT = not assigned. Significant differences between grazing treatment indicated by *($p < 0.05$), non significant results as *ns* ($p > 0.05$), Wilcoxon matched pairs test.

4.4.8 Environmental factors that influence invertebrate habitat choice

The RDA triplot (Figure 4.6) shows a visual interpretation of the relationship between eight environmental variables, selected by Monte Carlo forward selection, and the distribution of functional groups or prey capture methods. Axis 1 explained 79 % of the variation in functional group or prey capture method occurrence, axis 1 and 2 combined explained 89 % of the variation. The Monte Carlo test for all axes was significant for three environmental variables; temperature (positively correlated with axis 1: F-ratio = 23.73, $P < 0.01$), vegetation height (negatively correlated with axis 2: F-ratio = 3.59, $P < 0.05$) and salinity (positively correlated with axis 2: F-ratio = 2.38, $P < 0.05$), all other environmental variables either correlated with these three or did not describe a significant proportion of the variation in functional group occurrence. Grazing intensity was clearly separated out by axis 1, with all grazed experimental units positively associated with and all un-grazed units negatively associated with axis 1. Predatory, zoophagus, and detritivorous Coleoptera were all negatively associated with axis 1, as were foliage running hunters, space web builders and zoophagus and phytophagus other invertebrates. Predatory Hemiptera and sheet weaving spiders were positively associated with axis 1. Phytophagus Hemiptera and ground running hunter spiders were negatively associated with axis 2, not assigned Coleoptera and other detritivores were positively associated with axis 2.

4.4.9 Food web analysis

Large detritivores, mainly Orchestia and woodlice, accounted for 71 % of all the invertebrates sampled on the un-grazed marsh, 17 % on the grazed marsh (Figure 4.7). Small detritivores, predominantly collembola, accounted for only 6 % on the un-grazed marsh compared to 38 % on the grazed marsh. Large crane flies were more numerous on the grazed marsh (7 %). Small flies and mites were abundant in both grazing treatments. Large and medium predatory beetles accounted for 6 % of all invertebrates on the un-grazed marsh, 2 % on the grazed marsh. Medium hunting spiders were present in equal proportions on both marsh types (2 %). Small Linyphiidae were much more abundant, both in total and proportional abundance,

on the grazed marsh (13 %) compared to the un-grazed marsh (3 %). Predatory shore bugs were only present on the grazed marsh (2 %).

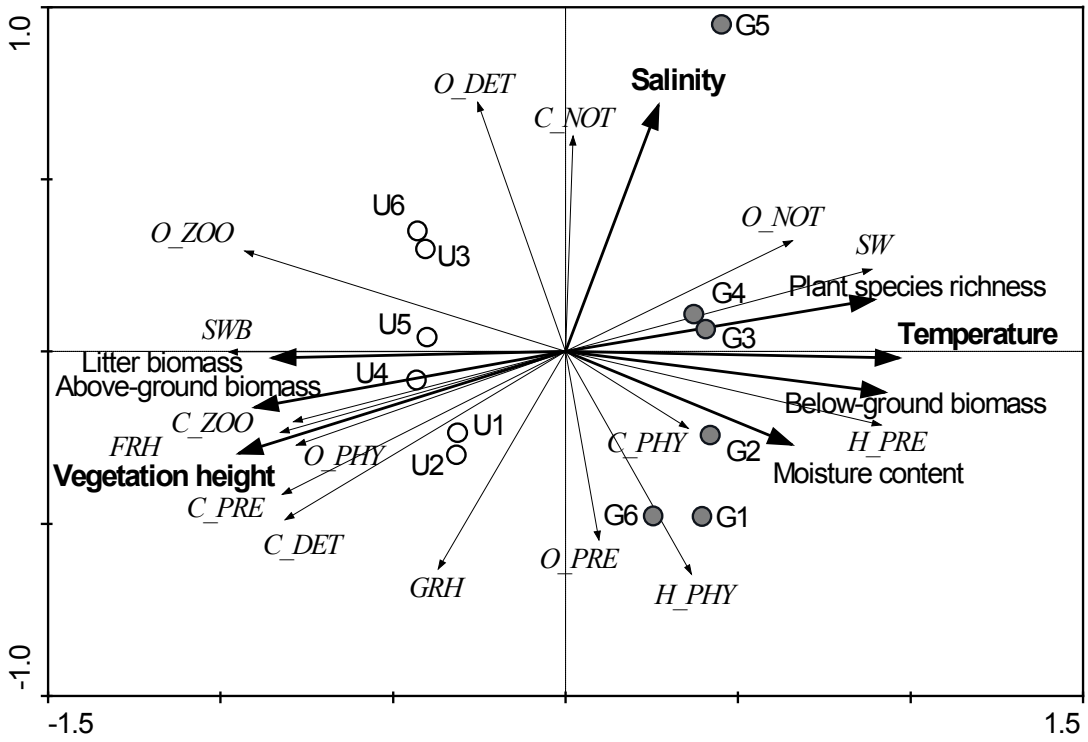

Figure 4.6 RDA triplot showing the relationship between eight environmental variables and the distribution of sixteen functional groups and prey capture methods. Environmental variables were selected by forward selection (Canoco v.4.5; Monte Carlo test, 500 permutations); the three significant ones, temperature, vegetation height and salinity are shown in bold. Grazed experimental units (G1-G6) are displayed as grey circles, un-grazed units (U1-U6) as white circles.

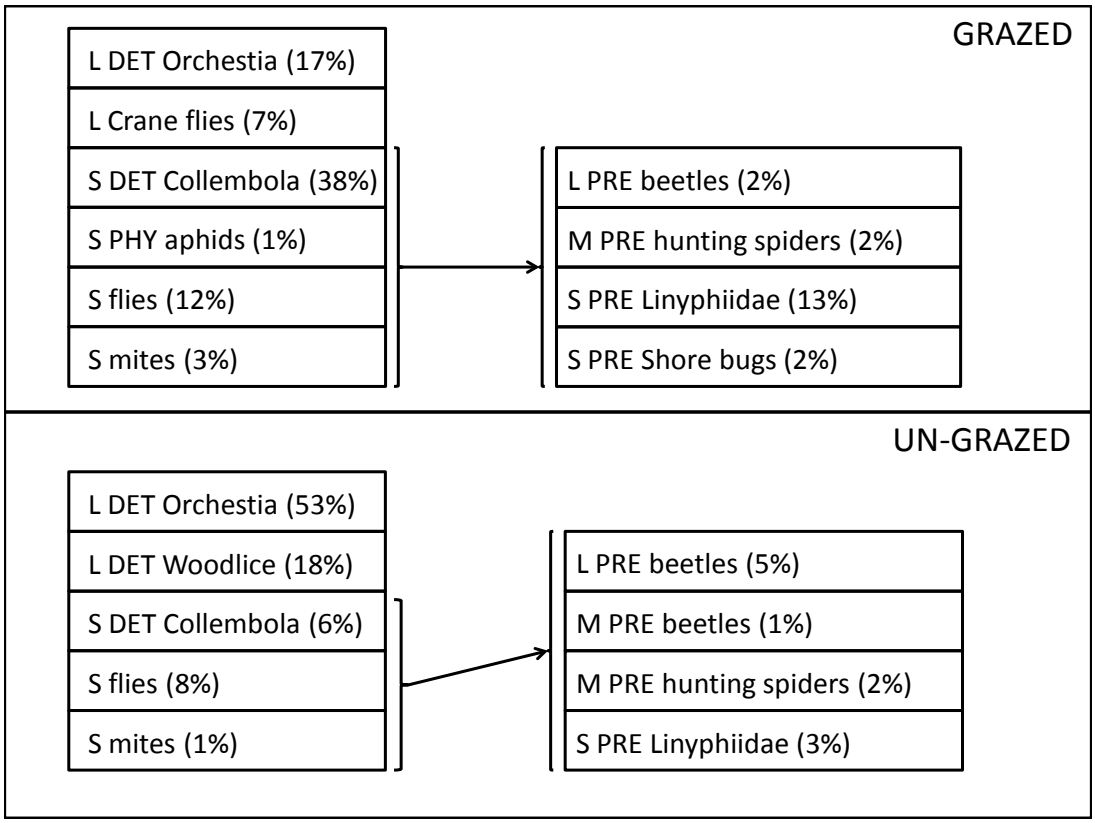

Figure 4.7 Ground dwelling invertebrate food web for cattle grazed and un-grazed salt marsh. Body length of invertebrates: L (large ≤ 30 mm), M (medium ≤ 20 mm), S (small ≤ 10 mm). Functional group of invertebrates: DET = detritivore, PHY = phytophagus, PRE = predatory (L PRE beetles also include zoophagus beetles). Invertebrate abundance is expressed as percentage of total invertebrates per grazing treatment.

4.5 Discussion

4.5.1 Overview

This study focused on the impact of cattle grazing on the abundance, diversity and functional group structure of the entire ground dwelling saltmarsh invertebrate community. Our results indicate that overall invertebrate abundance was greater on the un-grazed marsh. This finding is in line with evidence from other grassland and saltmarsh systems (Andresen *et al.* 1990; Bakker et al. 1993; Morris 2000). Coastal specialist abundance was greatest on the uniformly short sward cattle grazed salt marsh. European saltmarsh conservation often involves livestock grazing to improve plant diversity and provide a suitable habitat for over-wintering

breeding birds and invertebrate coastal specialists. Here we argue that un-grazed areas of marsh also have a conservation value in their own right. As well as higher invertebrate abundance the functional structure of the un-grazed marsh is also different from the grazed marsh, with many large predators and detritivores present. The grazed marsh was characterised by high plant species richness, short vegetation, limited plant litter and warm compact soil prone to water-logging. The un-grazed marsh was dominated by *E. repens*, leading to a deep plant litter layer and drier less compact soil than the grazed marsh. Vegetation height diversity did not differ between grazing treatments.

4.5.2 Coleoptera, Hemiptera & Araneae

Coleoptera abundance and species richness was much higher on the un-grazed marsh. This may be due to reduced physical disturbance of the habitat. Duffey (1975) showed that even moderate trampling by humans of five treads a month, to simulate cattle treading, reduced Coleoptera abundance by 82 % after a year compared to an un-trampled control. Coleoptera also lack submersion resistance (Rothenbücher & Schaefer, 2006), relevant as un-grazed marshes are drier habitats than grazed marshes due to plant litter build up and reduced waterlogging. Large and medium sized predatory, zoophagus and detritivorous beetles were very abundant on the tall un-grazed marsh, in contrast small predatory Hemiptera preferred the short, moist vegetation of the grazed marsh. Large invertebrates favour the un-grazed marsh as birds select larger invertebrates when feeding so tall vegetation is likely to provide cover from this type of predation, small predatory invertebrates prefer the grazed marsh due to reduced competition from larger invertebrate predators (Enders, 1975; Lassau *et al*., 2005). Detritivorous beetles are associated with the un-grazed marsh due to the availability of greater amounts of plant detritus than the grazed marsh.

Overall spider abundance was greater on the grazed marsh due to the predominance of small sheet weaving Linyphiidae spiders. Foliage running hunters and space web builders were more abundant on the un-grazed marsh. Ground running hunters were slightly more abundant on the un-grazed marsh. These

differences can largely be explained by structural differences between the two marsh types. *Erigone atra*, *Oedothorax fuscus*, *Oedothorax retusus* and *Savignya frontata*, all active Linyphiidae aeronauts, are found in much greater numbers on the grazed marsh than the un-grazed marsh, partly due to their ability to disperse into open or disturbed habitats, such as grazed land, where competition from larger invertebrate predators is low (Bell *et al*., 2001; Gibson *et al*., 1992b). Prey availability and preference for wetter habitats may also explain why Linyphiidae prefer the grazed marsh. Erigonine Linyphiidae, around half the sheet weavers sampled from the grazed marsh, are less than 2 mm long and feed on Collembola and small flies, an abundant food source on the grazed marsh (Enders, 1975; Figure 4.6). Another sheet weaver, *Hypomma bituberculatum*, was very abundant on the grazed marsh, it survives submersion in fresh water (Harvey *et al.*, 2002) and can therefore compete with other spider species in waterlogged plots. The comb spider *Robertus lividus*, a space web builder, was found only on the un-grazed marsh where litter levels were greatest as in Harvey *et al.* (2002). The foliage running hunter, *Clubiona stagnatilis,* was more abundant on tall un-grazed marsh. The most common ground running hunter species, *P. purbeckensis*, did not show a clear habitat preference but two other Lycosids, *Pardosa pullata* and *Pirata piraticus* were more abundant on the un-grazed marsh. It is worth noting that the use of pitfall traps to sample ground dwelling invertebrates will lead to under representation of certain spider groups, such as orb weavers, dependent upon the vertical structure of upper foliage layers.

4.5.3 Other invertebrates

Previously mentioned predatory groups, Coleoptera, Hemiptera and Araneae were often closely associated with a particular marsh type. In contrast, all other predatory invertebrates, parasitoid wasps, were equally abundant between grazing treatments. Parasitoid wasps are a diverse group providing a key ecosystem service in the regulation of insect populations (Fraser *et al.,* 2008), as active fliers this group was less influenced by ground level environmental variables. Zoophagus invertebrates were significantly more abundant on the un-grazed marsh. Dennis *et al.* (2001) found that in upland grasslands most harvestmen tended to prefer un-

grazed or sheep grazed to cattle grazed swards. The crane flies, Tipulidae, were much more abundant on the grazed marsh, in line with Cole *et al*.'s findings (2010) from grazed uplands. Large detritivores such as woodlice and the sand hopper, *O. gammerella,* were much more abundant on the un-grazed marsh due to the high level of plant detritus available as combined food source and shelter. Small detritivores such as Collembola were most abundant on the grazed marsh as in Meyer *et al*. (1995). They are able to proliferate here as they can survive anoxia in water-logged habitats by utilising passive drifting, a dormant egg stage and plastron respiration (Marx *et al*., 2009).

4.5.4 Abundance of coastal specialist species

For carabid inter-tidal coastal specialists *B. minimum* and *D. gustavii* the grazed marsh provided a more suitable habitat than the un-grazed marsh, as in Pétillon *et al.* (2007; 2008). The rove beetle *B. marina* also preferred the grazed marsh. In contrast, *B. iricolor* was more abundant on the un-grazed marsh. The Hemipteran nationally scarce invertebrate *Saldula opacula* was only present on the grazed marsh. For Araneae, coastal Linyphiidae specialists, *E. longipalpis* and *S. ambiguuus*, were much more abundant on the grazed marsh, as in Pétillon *et al.* (2005; 2007).

4.6 Conclusion

Soil temperature, bulk density and moisture content were higher on the grazed marsh. Plant species richness and below-ground root biomass were greater on the grazed marsh. Percentage cover of *E. repens*, above-ground plant biomass and litter biomass, were all significantly higher on the un-grazed marsh. Management of salt marshes for the conservation of invertebrates should aim to strike a balance between preserving maximum invertebrate diversity and abundance and maintaining a habitat suitable for coastal specialists. Un-grazed salt marshes provide a suitable habitat for an abundant and diverse invertebrate community, but cattle grazed marshes with short swards support a greater abundance and diversity of nationally scarce saltmarsh or inter-tidal coastal specialist species. The saltmarsh food web also differs markedly with grazing intensity. The un-grazed marsh is dominated by large detritivores and predatory beetles; the grazed marsh by smaller

detritivores and Linyphiidae spiders adapted to open or disturbed habitats. Grazing intensity influences two key drivers of invertebrate habitat choice, vegetation height and soil temperature, via vegetation removal and soil compaction. Particular species, functional groups or coastal specialists respond differently to these variables. Therefore, the provision of both un-grazed and short sward cattle grazed habitat is important to salt marsh invertebrate conservation management.

4.7 Acknowledgements

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4.9 Appendix

Table A4.1. Total counts of all invertebrates sampled from grazed 'G' and un-grazed 'U' marsh. Order, family, species, species authority and common name are listed alongside functional group, prey capture method and coastal specialist information in the 'Group' column (evidence for functional group assignment from list of superscript numbers). Order: COL = Coleoptera, HET = Heteroptera, HOM = Homoptera (Heteroptera and Homoptera both sub-orders of Hemiptera), ARA = Araneae, HYM = Hymenoptera, OPI = Opilones, PUL = Pulmonata, LEP = Lepidoptera, HAP = Haplotaxida, COLL = Collembola, ISO = Isopoda, AMP = Amphipoda, ACA = Acarina, DIP = Diptera, + includes larvae, L = larvae only. Group: PRE = predatory, ZOO = zoophagus, PHY = phytophagus, DET = Detritivore (DET (S) = scavenging, DET (F) = fungivorous), NOT = not assigned, FRH = foliage running hunter, GRH = ground running hunter, SWB = Space web builder, SW = Sheet weaver, CS = coastal specialist, N = notable species associated with salt marsh. Invertebrate nomenclature follows Duff (2008) for Coleoptera and Fauna Europea (2011) for all other invertebrates.

Order	Family	Species	Species authority	Common name	Group	G	U
COL	Staphylinidae	*Tachinus rufipes*	Linnaeus,1758	Rove beetle	PRE[1*]	0	30
COL	Staphylinidae	*Tachyporus nitidulus*	Fabricius, 1781	Rove beetle	PRE[1]	0	2
COL	Staphylinidae	*Tachyporus pusillus*	Gravenhorst, 1806	Rove beetle	PRE[1]	0	5
COL	Staphylinidae	*Amischa analis*	Gravenhorst, 1802	Rove beetle	PRE[1]	0	3
COL	Staphylinidae	*Cordalia obscura*	Gravenhorst, 1802	Rove beetle	PRE[1]	14	394
COL	Staphylinidae	*Oxypoda brachyptera*	Stephens, 1832	Rove beetle	PRE[1*]	33	56
COL	Staphylinidae	*Oxypoda procerula*	Mannerheim, 1830	Rove beetle	PRE[1*]	2	3
COL	Staphylinidae	*Stenus palustris*	Erichson, 1839	Rove beetle	PRE[1*]	2	0
COL	Staphylinidae	*Stenus fulvicornis*	Stephens, 1833	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Stenus bimaculatus*	Gyllenhal, 1810	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Stenus canaliculatus*	Gyllenhal, 1827	Rove beetle	PRE[1]	1	1
COL	Staphylinidae	*Stenus clavicornis*	Scopoli, 1763	Rove beetle	PRE	0	5
COL	Staphylinidae	*Stenus juno*	Paukull, 1789	Rove beetle	PRE[1]	2	7
COL	Staphylinidae	*Stenus brunnipes*	Stephens, 1833	Rove beetle	PRE[1*]	3	54
COL	Staphylinidae	*Lathrobium fulvipenne*	Gravenhorst, 1806	Rove beetle	PRE[1]	9	173
COL	Staphylinidae	*Lathrobium geminum*	Kraatz, 1857	Rove beetle	PRE[1*]	5	125
COL	Staphylinidae	*Sunius propinquus*	Brisout, 1867	Rove beetle	PRE[1*]	0	1
COL	Staphylinidae	*Othius laeviusculus*	Stephens, 1833	Rove beetle	PRE[1*]	4	0
COL	Staphylinidae	*Gabrius osseticus*	Kolenati, 1846	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Philonthus carbonarius*	Gravenhorst, 1802	Rove beetle	PRE[1]	13	0
COL	Staphylinidae	*Philonthus cognatus*	Stephens, 1832	Rove beetle	PRE[1]	2	4
COL	Staphylinidae	*Philonthus umbratilis*	Gravenhorst, 1802	Rove beetle	PRE[1]	2	0
COL	Staphylinidae	*Quedius fuliginosus*	Gravenhorst, 1802	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Quedius levicollis*	Brullé, 1832	Rove beetle	PRE[1*]	45	45
COL	Staphylinidae	*Quedius semiaeneus*	Stephens, 1833	Rove beetle	PRE[1*]	0	1
COL	Staphylinidae	*Ocypus aenocephalus*	De Geer, 1774	Rove beetle	PRE[1*]	0	1
COL	Staphylinidae	*Xantholinus linearis*	Olivier, 1795	Rove beetle	PRE[1]	4	1
COL	Staphylinidae	*Xantholinus longiventris*	Heer, 1839	Rove beetle	PRE[1]	7	89
COL	Coccinellidae	*Anisosticta*	Linnaeus,1758	Lady bird	PRE[2]	2	0

		novemdecimpunctata					
COL	Coccinellidae	*Coccinella undecimpunctata*	Linnaeus,1758	Lady bird	PRE[2]	16	0
COL	Staphylinidae	*Tasgius globulifer*	Geoffroy, 1785	Rove beetle	PRE[3*]	1	26
COL	Staphylinidae	*Tasgius ater*	Gravenhorst, 1802	Rove beetle	PRE[3*]	0	1
COL	Cantharidae+	*Cantharis rufa*	Linnaeus,1758	Soldier beetle	PRE[2]	176	533
COL	Carabidae	*Loricera pilicornis*	Fabricius, 1775	Ground beetle	ZOO[4]	25	4
COL	Carabidae	*Clivina fossor*	Linnaeus,1758	Ground beetle	ZOO[4]	0	4
COL	Carabidae	*Dyschirius globosus*	Herbst, 1784	Ground beetle	ZOO[4]	0	2
COL	Carabidae	*Trechus quadristriatus*	Schrank, 1781	Ground beetle	ZOO[4]	0	1
COL	Carabidae	*Bembidion lampros*	Herbst, 1784	Ground beetle	ZOO[4]	0	1
COL	Carabidae	*Bembidion varium*	Olivier, 1795	Ground beetle	ZOO[4*]	20	3
COL	Carabidae	*Bembidion assimile*	Gyllenhal, 1810	Ground beetle	ZOO[4*]	17	269
COL	Carabidae	*Bembidion minimum*	Fabricius, 1792	Ground beetle	ZOO[4*] (CS)	64	4
COL	Carabidae	*Bembidion aeneum*	Germar, 1842	Ground beetle	ZOO[4]	246	267
COL	Carabidae	*Bembidion iricolor*	Bedel, 1879	Ground beetle	ZOO[4*] (CS)	13	517
COL	Carabidae	*Pterostichus niger*	Schaller, 1783	Ground beetle	ZOO[4]	3	162
COL	Carabidae	*Pterostichus minor*	Gyllenhal, 1827	Ground beetle	ZOO[4*]	20	148
COL	Carabidae	*Pterostichus nigrita*	Paykull, 1790	Ground beetle	ZOO[4]	0	2
COL	Carabidae	*Pterostichus diligens*	Sturm, 1824	Ground beetle	ZOO[4]	0	126
COL	Carabidae	*Olisthopus rotundatus*	Paykull, 1790	Ground beetle	ZOO[4]	9	5
COL	Carabidae	*Agonum marginatum*	Linnaeus,1758	Ground beetle	ZOO[4]	2	0
COL	Carabidae	*Agonum viduum*	Panzer, 1796	Ground beetle	ZOO[4]	0	1
COL	Carabidae	*Dicheirotrichus gustavii*	Crotch, 1871	Ground beetle	ZOO[5] (CS)	32	1
COL	Carabidae	*Demetrias atricapillus*	Linnaeus, 1758	Ground beetle	ZOO[4]	1	0
COL	Carabidae	*Amara communis*	Panzer, 1797	Ground beetle	PHY[4]	0	18
COL	Carabidae	*Harpalus rufipes*	De Geer, 1774	Ground beetle	PHY[4]	0	5
COL	Carabidae	*Harpalus affinis*	Schrank, 1781	Ground beetle	PHY[4]	1	0
COL	Staphylinidae	*Carpelimus corticinus*	Gravenhorst, 1806	Rove beetle	PHY[1]	0	1
COL	Chrysomelidae	*Chrysolina staphylaea*	Linnaeus, 1758	Leaf eater	PHY[2]	1	15
COL	Chrysomelidae	*Phaedon armoraciae*	Linnaeus, 1758	Leaf eater	PHY[2]	0	2
COL	Chrysomelidae L			Leaf eater	PHY[2]	3	10
COL	Apionidae	*Protapion fulvipes*	Geoffroy, 1785	Weevil	PHY[6]	4	0
COL	Erirhinidae	*Notaris scirpi*	Fabricius, 1793	Weevil	PHY[7]	8	6
COL	Helophoridae	*Helophorus brevipalpis*	Bedel, 1881	Water beetle	PHY[8]	64	18
COL	Hydraenidae	*Ochthebius dilatatus*	Stephens, 1829	Aquatic beetle	PHY[9]	72	24
COL	Byturidae	*Byturus ochraceus*	Scriba, 1790	Fruit beetle	PHY[10]	12	5
COL	Staphylinidae	*Omalium caesum*	Gravenhorst, 1806	Rove beetle	DET[1]	0	3
COL	Staphylinidae	*Micropeplus staphylinoides*	Marsham, 1802	Rove beetle	DET (F)[1]	0	3
COL	Staphylinidae	*Ischnosoma splendidum*	Gravenhorst, 1806	Rove beetle	DET (F)[1]	5	39
COL	Staphylinidae	*Sepedophilus marshami*	Stephens, 1832	Rove beetle	DET (F)[1]	0	71
COL	Staphylinidae	*Atheta graminicola*	Gravenhorst, 1806	Rove beetle	DET (F)[1]	1	0
COL	Staphylinidae	*Atheta triangulum*	Kraatz, 1856	Rove beetle	DET (F)[1]	2	0
COL	Staphylinidae	*Atheta* (other)		Rove beetle	DET (F)[1]	3	15
COL	Staphylinidae	*Anotylus rugosus*	Fabricius, 1775	Rove beetle	DET[1]	2	3
COL	Leiodidae	*Catops morio*	Fabricius, 1787	Fungus beetle	DET (S)[6]	0	8
COL	Cryptophagidae	*Atomaria atricapilla*	Stephens, 1830	Fungus beetle	DET (F)[11]	0	1
COL	Cryptophagidae	*Atomaria fuscata*	Schöenherr, 1808	Fungus beetle	DET (F)[11]	0	1
COL	Lathridiidae	*Corticaria punctulata*	Marsham, 1802	Mould beetle	DET[11]	1	7

COL	Lathridiidae	*Corticarina minuta*	Fabricius, 1792	Mould beetle	DET[11]	0	2
COL	Staphylinidae	*Lesteva sicula heeri*	Fauvel, 1871	Rove beetle	DET (S)[12]	0	5
COL	Staphylinidae	*Lesteva longoelytrata*	Goeze, 1777	Rove beetle	DET (S)[12]	1	0
COL	Hydrophilidae	*Cercyon impressus*	Fabricius, 1775	Water beetle	DET[13]	0	2
COL	Hydrophilidae	*Megasternum concinnum*	Marsham, 1802	Water beetle	DET[13]	17	111
COL	Hydrophilidae	*Sphaeridium scarabaeoides*	Linnaeus,1758	Water beetle	DET[13]	1	0
COL	Ptiliidae	*Ptenidium Sp.*		Feather beetle	DET (F)[13]	0	1
COL	Ptiliidae	*Acrotrichis Sp.*		Feather beetle	DET (F)[13]	2	67
COL	Staphylinidae	*Brundinia marina*	Mulsant & Rey, 1853	Rove beetle	NOT (CS)	172	111
COL	Staphylinidae	*Mocyta fungi*	Gravenhorst, 1806	Rove beetle	NOT	58	25
COL	Carabidae L				NOT	32	3
COL	Staphylinidae L				NOT	0	108
HET	Nabidae	*Stalia major*	Costa, 1841	Damsel bug	PRE[14]	0	1
HET	Nabidae	*Nabis lineatus*	Dahlbom, 1851	Damsel bug	PRE[14]	0	3
HET	Dipsocoridae	*Ceratocombus coleoptratus*	Zetterstedt, 1819		PRE[11]	0	13
HET	Saldidae	*Saldula opacula*	Zetterstadt, 1838	Shore bug	PRE[15*] (N)	28	0
HET	Saldidae	*Saldula pallipes*	Fabricius, 1794	Shore bug	PRE[15*]	4	0
HET	Saldidae+	*Salda littoralis*	Linnaeus, 1758	Shore bug	PRE[16]	638	2
HOM	Cicadellidae	*Aphrodes albifrons*	Linnaeus, 1758	Leaf hopper	PHY[17]	0	1
HOM	Cicadellidae	*Aphrodes bicinctus*	Schrank, 1776	Leaf hopper	PHY[17]	1	5
HOM	Cicadellidae	*Arthaldeus pascuellus*	Fallen, 1826	Leaf hopper	PHY[17]	5	1
HOM	Cicadellidae	*Psammotettix putoni*	Then, 1898	Leaf hopper	PHY[17]	12	0
HOM	Cicadellidae	*Conosanus obsoletus*	Kirshbaum, 1858	Leaf hopper	PHY[17]	6	3
HOM	Cicadellidae	*Streptanus sordidus*	Zetterstedt, 1828	Leaf hopper	PHY[17]	7	0
HOM	Cicadellidae	*Macrosteles viridigriseus*	Edwards, 1922	Leaf hopper	PHY[17]	5	0
HOM	Delphacidae	*Javesella dubia*	Kirschbaum, 1868	Leaf hopper	PHY[17]	1	2
HOM	Delphacidae+	*Javesella pellucida*	Fabricius, 1794	Leaf hopper	PHY[17]	0	29
HOM	Stenorrhyncha			Aphids only	PHY[17]	173	102
HET	Miridae	*Megaloceraera recticornis*	Geoffroy, 1785	Mirid bug	PHY[15]	0	1
HOM	Cicadellidae L	Cicadellidae larvae			PHY[17]	66	5
ARA	Clubionidae	*Clubiona stagnatilis*	Kulczynski, 1897	Foliage spider	PRE (FRH)[18]	3	25
ARA	Gnaphosidae	*Micaria pulicaria*	Sundevall, 1831	Ground spider	PRE (GRH)[18]	0	15
ARA	Lycosidae	*Trochosa ruricola*	De Geer, 1778	Wolf spider	PRE (GRH)[18]	12	49
ARA	Lycosidae	*Pardosa purbeckensis*	Cambridge, 1895	Wolf spider	PRE (GRH)[18] (CS)	454	515
ARA	Lycosidae	*Pardosa pullata*	Clerck, 1757	Wolf spider	PRE (GRH)[18]	2	22
ARA	Lycosidae	*Pirata piraticus*	Clerck, 1757	Wolf spider	PRE (GRH)[18]	5	73
ARA	Tetragnathidae	*Pachygnatha clercki*	Sundevall, 1823	-	PRE (GRH)[21]	73	153
ARA	Tetragnathidae	*Pachygnatha degeeri*	Sundevall, 1830	-	PRE (GRH)[21]	106	1
ARA	Theridiidae	*Robertus lividus*	Blackwall, 1836	Comb spider	PRE (SWB)[18]	0	153
ARA	Linyphiidae	*Walckenaeria nudipalpis*	Westring, 1851	Money spider	PRE (SW)[18]	0	1
ARA	Linyphiidae	*Walckenaeria vigilax*	Blackwall, 1853	Money spider	PRE (SW)[18]	33	9
ARA	Linyphiidae	*Walckenaeria incisa*	Cambridge, 1871	Money spider	PRE (SW)[18]	1	0
ARA	Linyphiidae	*Walckenaeria kochi*	Cambridge, 1873	Money spider	PRE (SW)[18]	21	37

ARA	Linyphiidae	*Walckenaeria acuminata*	Blackwall, 1833	Money spider	PRE (SW)[18]	0	83
ARA	Linyphiidae	*Hypomma bituberculatum*	Wider, 1834	Money spider	PRE (SW)[18]	243	58
ARA	Linyphiidae	*Oedothorax fuscus*	Blackwall, 1834	Money spider	PRE (SW)[18]	1086	13
ARA	Linyphiidae	*Oedothorax retusus*	Westring, 1851	Money spider	PRE (SW)[18]	156	9
ARA	Linyphiidae	*Silometopus ambiguus*	Cambridge, 1905	Money spider	PRE (SW)[18](CS)	273	15
ARA	Linyphiidae	*Savignia frontata*	Blackwall, 1833	Money spider	PRE (SW)[18]	242	104
ARA	Linyphiidae	*Araeoncus humilis*	Blackwall, 1841	Money spider	PRE (SW)[18]	1	0
ARA	Linyphiidae	*Erigone dentipalpis*	Wider, 1834	Money spider	PRE (SW)[18]	1	0
ARA	Linyphiidae	*Erigone atra*	Blackwall, 1833	Money spider	PRE (SW)[18]	177	1
ARA	Linyphiidae	*Erigone longipalpis*	Sundevall, 1830	Money spider	PRE (SW)[18] (CS)	2213	9
ARA	Linyphiidae	*Leptorhoptrum robustum*	Westring, 1851	Money spider	PRE (SW)[18]	10	4
ARA	Linyphiidae	*Centromerita concinna*	Thorell, 1875	Money spider	PRE (SW)[18]	0	26
ARA	Linyphiidae	*Bathyphantes approximatus*	Cambridge, 1871	Money spider	PRE (SW)[18]	6	9
ARA	Linyphiidae	*Bathyphantes gracilis*	Blackwall, 1841	Money spider	PRE (SW)[18]	70	27
ARA	Linyphiidae	*Bathyphantes parvulus*	Westring, 1851	Money spider	PRE (SW)[18]	0	7
ARA	Linyphiidae	*Tenuiphantes tenuis*	Blackwall, 1852	Money spider	PRE (SW)[18]	67	143
ARA	Linyphiidae	*Palliduphantes tenuis*	Cambridge, 1871	Money spider	PRE (SW)[18]	0	1
ARA	Linyphiidae	*Allomengea scopigera*	Grube, 1859	Money spider	PRE (SW)[18]	25	1010
HYM	Parasitic Hymenoptera			Parasitoid wasp	PRE[19]	623	615
OPI				Harvestmen	ZOO[19]	1	68
PUL				Snail	PHY[19]	7	78
LEP				Moth larvae	PHY[19]	21	22
HAP	Enchytraeidae			Pot worm	DET[20]	147	0
COLL				Springtail	DET[19]	13857	3391
ISO				Woodlice	DET (S)[19]	76	9539
AMP	Talitridae	*Orchestia gammarella*	Pallas, 1766	Sandhopper	DET (S)[19]	6133	27773
ACA				Mite	NOT	1168	563
HYM	Formicidae			Ant	NOT	18	4
DIP	Tipulidae+			Crane fly	NOT	2461	56
DIP	Other Diptera				NOT	4078	4087
DIP	Limoniidae L				NOT	29	0
DIP	Stratiomyidae L				NOT	48	3
DIP	Ephaedridae L				NOT	29	0
DIP	Scatophagidae L				NOT	48	0
DIP	Other fly larvae				NOT	281	37

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Chapter 5: Methane, carbon dioxide and nitrous oxide fluxes from a temperate salt marsh: grazing management does not alter Global Warming Potential

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5.1 Abstract

Soil greenhouse gas emissions from cattle grazed and un-grazed temperate upper salt marsh were measured using dark static chambers, monthly for one year. Additionally, below-ground gas sampling tubes were used to measure soil methane (CH_4) concentrations. CH_4 efflux from grazed and un-grazed salt marsh did not differ significantly, however grazing did lead to 'hotspots' of underground CH_4 (up to 6 % of total air volume) and CH_4 efflux (peak of 9 mg m^{-2} h^{-1}) significantly linked to high soil moisture content, low soil temperatures and the presence of *Juncus gerardii*. Carbon dioxide (CO_2) efflux was greater from the un-grazed marsh (mean of 420 mg m^{-2} h^{-1}) than the grazed marsh (mean of 333 mg m^{-2} h^{-1}) throughout most of the year and was positively correlated with deeper water table and greater soil temperatures. Grazing was not a significant predictor of nitrous oxide (N_2O) soil emissions. Global Warming Potential (GWP; over 100 years), calculated from mean yearly chamber fluxes for CH_4 and CO_2, did not differ significantly with grazing treatment. Seasonal variation in the key drivers of soil greenhouse gas efflux; soil temperature, moisture and water table, plus the presence or absence of aerenchymatous plants such as *J. gerardii* were more important to the magnitude of greenhouse gas emissions than grazing management *per se*.

Key words: chamber flux measurements**,** greenhouse gases**,** salt marshes**,** livestock grazing**,** UK: Ribble estuary

5.2 Introduction

Methane (CH_4), carbon dioxide (CO_2), and nitrous oxide (N_2O) are all major greenhouse gases. Despite natural wetlands accounting for a third of global CH_4 flux, their contribution to Global Warming Potential (GWP) may be off-set by their carbon sink capabilities and minimal N_2O emissions (Dassonville & Renault, 2002; Denman *et al*., 2007; Lai, 2009). Managing wetlands to minimise their GWP is therefore crucial. Most previous research focuses on freshwater wetlands such as peatlands (Le Mer & Roger, 2001; Limpens *et al*., 2008; Lai, 2009) with the GWP of coastal habitats such as tidal flats and salt marshes remaining less well quantified (Pacyna & Manø, 2006). European salt marshes are often managed by livestock grazing to provide a suitable habitat for over-wintering bird species (Adam, 1990; Milsom *et al*., 2000; Chatters, 2004), however, the impact of this management on the GWP of this habitat is not well known. Grazing management is expected to have clear implications for GWP as soil moisture content, soil temperature and plant community composition, all key drivers of soil greenhouse gas emissions, often differ with grazing intensity (Bakker *et al*., 1993; Curry, 1994; Lambert, 2000). Despite the fact that salt marshes are by definition inter-tidal wetlands, their upper zones share many characteristics of semi-natural grasslands due to infrequent inundation. Aerated grassland soils are large carbon stores, produce little CH_4 and emit significant amounts of N_2O only under intensive grazing or fertiliser input regimes (Soussana *et al*., 2007; Allard *et al*., 2007; Del Grosso, 2010). Upper temperate salt marshes, common throughout Europe and characteristic of the vast area behind summer dykes in the Wadden Sea area of Germany (Bakker *et al*., 1993), may therefore have a similar GWP to terrestrial grasslands during the summer months if tidal inundation is rare.

CH_4 is produced by methanogenic archaea from either CO_2 or acetic acid when soil conditions are suitably anoxic (Denman *et al*., 2007). Where an oxic soil layer exists above an anoxic layer up to 88 % of CH_4 produced can be oxidised by

methanotrophs (Calhoun & King, 1997). CH_4 leaves the soil via three pathways, diffusion, ebullition and through the aerenchyma of certain plant species (Van der Nat & Middelburg, 2000). In wetland soils, CH_4 production is increased by standing water or waterlogged soil, high soil temperatures and increased organic matter or substrate availability (Le Mer & Roger, 2001; Ding *et al*., 2004; Kankaala *et al*., 2005). In the sulphate rich marine environment sulphate reducing bacteria typically out-compete methanogenic archaea in the anaerobic decomposition of organic matter, a process governed by the redox potential (Piker *et al*., 1998). As saltmarshes are tidal it is assumed that CH_4 emissions from this habitat are relatively insignificant. Bartlett *et al*. (1985) reported that North American coastal saltmarshes do not contribute significantly to CH_4 emissions. However, in a recent review of CH_4 emissions from temperate tidal marshes Poffenbarger *et al*. (2011) reported that while polyhaline tidal marshes had lower CH_4 emissions than fresh water marshes, oligohaline marshes had the highest and most variable emissions. To our knowledge, CH_4 efflux has not been measured for the upper zone of the salt marsh that may only be tidally inundated a dozen times a year. Cattle grazing may increase soil CH_4 emissions directly via the input of animal dung, a moderate CH_4 source, and indirectly via CH_4 ebullition caused by cattle trampling (IPCC, 1996; Lin *et al*., 2009; Herbst *et al*., 2011). In addition, grazed salt marshes may be prone to water-logged ground, have greater plant species richness than un-grazed marshes and are often characterised by *Juncus* species (rushes) that are known to vent CH_4 via their aerenchyma (Adam, 1990; Roslev & King, 1996; Lambert, 2000).

CO_2 efflux is comprised of microbial (soil) and plant respiration. Soil respiration requires aerobic decomposition conditions, intermediate soil moisture and becomes faster with increased soil temperature and ecosystem productivity (Luo & Zhou, 2006). Both European and North American saltmarshes have high levels of primary productivity (Vernberg, 1993; Mitsch & Gosselink, 2000) but exhibit variable redox potential and soil moisture regimes due to differences in timing and duration of tidal inundation. Regularly inundated salt marshes and mudflats are likely to show very different soil characteristics to upper salt marshes that are less frequently inundated. Studies of grazing and CO_2 efflux have largely concentrated

upon grassland systems. In Soussana *et al*. (2007) grasslands under widely differing grazing and fertiliser addition regimes were all net sinks of CO_2. However, livestock grazing may reduce plant respiration directly via removal of above-ground plant biomass by herbivores and also reduce soil respiration indirectly via decreased supply of readily available carbon to roots and microbes (Luo & Zhou, 2006). Despite this effect, 'hotspots' of CO_2 emissions from livestock dung, up to 50 % higher than control plots have been recorded (Lin *et al*., 2009) and should also be taken into account. Grazing intensity also influences soil carbon storage. Light, moderate or heavy grazing can all increase soil carbon, depending on grassland type (Kemp & Michalk, 2007). Conversely, extensively grazed or un-grazed grasslands may store more carbon than intensively managed grassland (Campbell *et al*., 1997; Soussana *et al*., 2004).

N_2O soil emissions occur where an aerobic soil surface layer coupled with an anaerobic layer immediately beneath provides suitable conditions for aerobic nitrifying bacteria to produce nitrate, from which anaerobic denitrifying bacteria produce N_2O (Mitsch & Gosselink, 2000). Nitrification may also occur in the oxidised root zone of plants. N_2O soil emissions are increased by high nitrate availability and compacted, waterlogged, warm soil (Van Groenigen *et al*., 2005; Lin *et al*., 2009; Del Grosso, 2010). In general, N_2O emissions are considered detrimental as they increase atmospheric pollution. However, in coastal systems, denitrification leading to increased N_2O efflux may be seen as environmentally beneficial, when this prevents the release of nitrate into the marine environment that can lead to eutrophication (Brin *et al*., 2010). There are very few studies concerning N_2O emissions from freshwater or saltwater wetland soils (Poffenbarger *et al*., 2011). Most studies from grasslands record greater soil N_2O emissions with increased livestock grazing intensities. Animal trampling leads to compact, warm, waterlogged soils, and the addition of animal waste a nitrate source, providing ideal conditions for soil N_2O efflux (Van Groenigen *et al*., 2005; Saggar *et al*., 2007; Lin *et al*., 2009; Del Grosso, 2010). However, Wolf *et al*. (2010) provides conflicting evidence, soil N_2O emissions were highest in un-grazed steppe grasslands and lowest in grasslands with highest stocking densities.

In this study we examine the effect of cattle grazing on greenhouse gas efflux and estimated GWP of a temperate upper saltmarsh. The following three hypotheses were examined: 1) Soil CH_4 efflux will be greater in the cattle grazed than the un-grazed salt marsh due to differences in compaction and soil moisture content; 2) Combined soil and plant CO_2 efflux will be greater in the un-grazed (aerobic, free draining soil with a large above-ground plant biomass) than the grazed marsh; 3) Soil N_2O efflux will be greater in the grazed than the un-grazed marsh due to differences in compaction, waterlogging and nitrate supply.

5.3 Study area, materials and methods

5.3.1 Crossens marsh

The salt marshes of the Ribble estuary cover 2000 ha in total. The study area, Crossens Marsh (53^o 41' 15" N, 2^o 57' 4" W), is located on the southern edge of the Ribble estuary in north-west England and is part of the Sefton Coast Special Protection Area managed by Natural England. The marsh has been arbitrarily split into two management types by a fence line that has been *in situ* for at least forty years, running more-or-less perpendicular to the shore. The grazed marsh is characterised by predominantly *Festuca rubra* saltmarsh National Vegetation Community (NVC; SM16d) and the un-grazed marsh by *Elytrigia repens* saltmarsh (SM28; Rodwell, 2000). The grazed part of the marsh covers 517 ha and is grazed uniformly by around 100 bullocks from late May to early October (0.2 cattle per hectare) to provide an overwintering feeding habitat for pink-footed geese (*Anser brachyrhynchus*). All experimental units were selected within the oligohaline (salinity = 0.5 – 5 PSU (practical salinity units)) high marsh zone where numerous creeks are present but tidal inundations are relatively rare, limited to around eight events a year on high equinox tides. A paired experimental design was used with six experimental units of approximately 10 m x 10 m set up on each side of a 600 m long section of the fence line, 100-150 m apart, in a 'mirror image' formation, giving six grazed (G1-G6) and six un-grazed (U1-U6) units (Figure 5.1). Each experimental unit was located between 20 m and 50 m from the fence line to ensure an

adequate buffer zone and checked for comparable elevation within ±10 cm. All measurements were carried out within these experimental units.

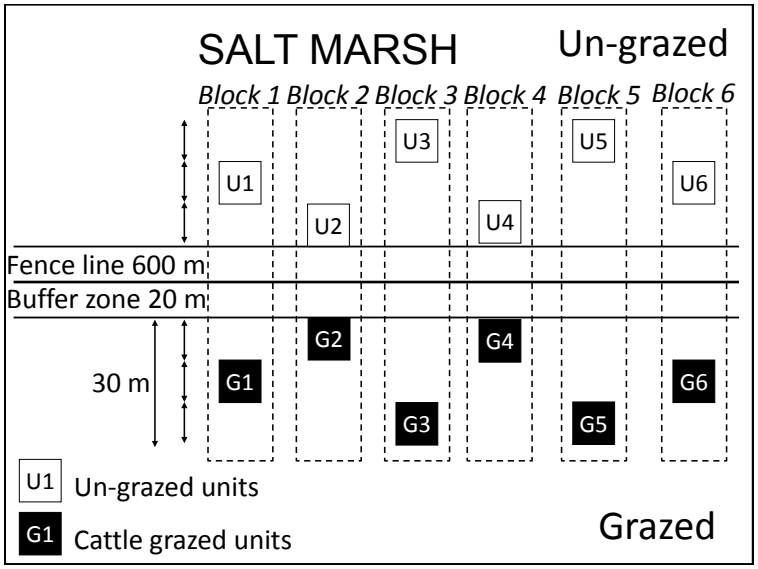

Figure 5.1 Experimental design at Crossens Marsh. All units are 10 m x 10 m square at 20 - 30 m, 30 - 40 m or 40 - 50 m from the fence line. Not to scale.

5.3.2 Marsh characterisation

The following measurements were taken for saltmarsh characterisation in 2009. Soil samples were collected during September from the top 15 cm of soil to measure salinity and pH. Soil was sieved to 2 mm and a sub sample of 10 g was taken from each sample and shaken with 25 ml of deionised water (1:2.5 dilution factor). A *Hanna* pH209 pH meter was used to measure pH and a *Jenway* 4520 Conductivity meter to measure electrical conductivity (mS cm^{-1}) as a proxy for salinity. Samples to determine bulk density and soil organic matter content were also collected using intact soil cores of 3.8 cm diameter and 15 cm depth. Cores were dried at 105 ^{o}C for 72 hours and the dry mass divided by the volume of the core to calculate bulk density. Loss-on-ignition was used to estimate organic matter content (Ball, 1964). Soil carbon stock in kg C m^{-2} was calculated from bulk density and the conversion factor of soil carbon as 0.55 of soil organic matter (Emmett *et al*., 2010). Soil moisture content and temperature were recorded at six locations within each experimental unit during September. Soil conductivity was measured in direct volts using a *Delta T* Theta Meter HH1 (four probes of 6 cm) and converted to

percentage soil moisture content using a calibration suitable for organic soils. Soil temperature was measured using a digital thermometer (single 11 cm probe). Vertical water infiltration rate, inversely related to waterlogged soil conditions, was measured using three single ring infiltrometers (Carroll *et al*., 2004) per experimental unit.

The potential for nutrient cycling by microbes was assessed using a measure of mineralisable N (Rowe *et al*., 2011). Three N mineralisation cores, 3.8 cm diameter and 15 cm depth, were taken from each experimental unit, during September. Soil cores were taken using plastic corers, capped at both ends to minimise soil disruption, and stored intact at 4 °C. Accumulated inorganic N was flushed from the cores by spraying with a solution of similar ionic concentration to UK rain over 7 days until 150 ml of leachate had been collected. Cores were incubated at 10 °C for 28 days, homogenised and a sub-sample extracted using 1 M KCl for the analysis of ammonium and nitrate content (Rowe *et al*., 2011). N mineralization rate was calculated over these 28 days assuming that all previous inorganic N had been removed during the 7 day flushing period. Mineralisable N was expressed as μg $N\ g^{-1}\ day^{-1}$ on both a dry soil weight and organic matter basis. The biological activity of soil meso-faunal decomposers, a proxy for aerobic soil activity, was measured using custom made bait lamina (Terra Protecta GmbH, Germany), 15 cm long with 16 holes filled with cellulose, bran and charcoal. Ten bait lamina per experimental unit were set up in two lines of five, 50 cm apart, pushed vertically into the ground so the top hole was 1 cm below the soil surface. Strips were placed in the ground in late June for 44 days and again in mid September for 34 days until 10 – 40 % of the bait had been degraded. Strips were removed, washed and each hole assessed for biological activity or 'feeding rate'. Feeding rates were standardised to percentage bait removed per 7 days.

Above-ground net primary productivity (ANPP), peak biomass from three grazer excluded areas per experimental unit, was recorded as a direct measure of primary productivity. At the beginning of March, vegetation was cut to ground level in three 50 cm x 50 cm areas per experimental unit. Each cut area was protected from cattle by an 8 cm mesh gabion (50 x 50 x 50 cm) and vegetation allowed to re-grow until

peak biomass at the end of August when areas were re-cut within a central 25 cm x 25 cm area. Vegetation was dried at 80 °C for 72 hours then weighed and converted to kg dry wt m^{-2} yr^{-1} to provide a measure of ANPP. Above-ground living plant material and plant litter were collected for five 25 cm x 50 cm quadrats per experimental unit in July, one root core of 5 cm diameter and 10 cm depth was also taken per quadrat and washed to remove all soil. Above-ground vegetation, litter and roots were all dried at 80 °C for 72 hours and weighed to give indicators of above-ground live plant biomass, litter biomass and below-ground root biomass respectively. Above-ground biomass can be linked to dark chamber respiration rates.

5.3.3 CH_4, CO_2 and N_2O chamber fluxes

Above-ground greenhouse gas fluxes were measured by a closed dark static chamber method. Each chamber consisted of a polyvinyl chloride (PVC) pipe of 15 cm height (30 cm internal diameter) with a rubber Septa sampling point located half way up, sealed to a 2 mm acrylonitrile butadiene styrene (ABS) lid, painted silver to reflect heat . These chambers were of similar diameter to those commonly used, but lower in height, and were chosen to increase the likelihood of measuring minor fluxes of CH_4 and N_2O by increasing the surface area to volume ratio. During measurement periods each static chamber was attached by a rubber seal to an in situ PVC pipe base (0.71 m^2). The base was placed firmly in the soil to a depth of 5 cm with 10 cm visible above-ground in June 2010, to give a combined chamber and base volume of 0.018 m^3. Vegetation and plant litter were not removed from within the chambers.

Two chambers per experimental unit, with bases 3 m apart, were used to measure daytime (between 11am and 3pm) greenhouse gas fluxes once a month for twelve months from September 2010 to August 2011. Gas samples were taken with a 30 ml syringe at 0, 30, 60, 90 and 120 minutes after chamber placement and immediately transferred to a 22 ml vial, over pressurised in the field but returned to lab pressure prior to analysis. Internal chamber temperature was recorded in two grazed and two un-grazed chambers per month using Tinytag data loggers (TGP-

4017 -40 to +85°C; Gemini Data Loggers). Gas analysis was carried out over the following three days using a Perkin Elmer Clarus 500 Gas Chromatograph (GC) with a Porapaq QS (80 – 100 mesh) analytical column and Turbomatrix 40 headspace autoanalyser. CO_2 and CH_4 were detected by FID, N_2O by ECD (at 375 °C, sample oven at 40 °C) to give ppm and peak area (mV) measurements for the three gases. The following standard gases were used to calibrate the GC, A: N_2O 1 ppm, CH_4 3.9 ppm, CO_2 995.5 ppm; B: N_2O 5.1 ppm, CH_4 50.4 ppm, CO_2 510.8 ppm; and C: N_2O 2 ppm, CH_4 20.3 ppm, CO_2 257.7 ppm. Samples were run after a calibration was achieved with an r^2 of > 0.99 for all three gases.

5.3.4 Flux calculation

Greenhouse gas fluxes were calculated from ppm and peak area measurements for each chamber using a GCflux model (Levy *et al*., 2011) run on Genstat 13.1 (Payne *et al*., 2011). For CO_2 and N_2O, fluxes were calculated for the full 0 to 120 minutes time scale (5 time points). For CH_4 fluxes the first time point (time 0) was excluded as it was often high compared with ambient air concentration (~1.8 ppm) due to probable ebullition from disturbance in placing the chamber as in Alm *et al*. (2007). The GCflux model calculated fluxes, with chamber volume and temperature accounted for, by five methods: 1) Simple averaging; 2) Linear regression; 3) Intercept method; 4) Negative exponential regression; 5) Asymptotic regression. Final model selection, and therefore flux output for further analysis, was based on the highest r^2 value. Within this study method 2) 'Linear regression' was consistently the best model fit for each data set. Regression values of $r^2 < 0.7$ were excluded unless they were indicative of low level or zero fluxes as in Waddington *et al*. (2010). Flux output in nmol m^{-2} s^{-1} was converted to mg m^{-2} h^{-1} for statistical analysis.

5.3.5 CH_4 soil concentration

Underground soil CH_4 concentrations were measured using plastic gas sampling tubes, 10 cm long, with an internal diameter of 16.5 mm, with 8 small holes (2.5 mm diameter) drilled at either 2.5 cm, 5 cm or 7.5 cm along the tube, depth when inserted in soil (Figure 5.2), to allow soil air at this depth to enter the tube. A

silicone bung was used to seal the base of the tube, a 17.5 mm Septa suba seal was attached to the top of each tube to allow gas sampling via syringe. The gas sampling tubes were installed in the field in July 2010, flush with the soil surface, three per experimental unit, one 2.5 cm, 5 cm and 7.5 cm, 5 cm apart in a triangle formation. Each set of tubes was protected by a rain hat and wire basket to prevent interference by cattle. The gas sampling tubes were allowed to equilibrate for one month to allow measurement of gas from the tubes to accurately reflect the soil concentration of CH_4 at each soil depth. Gas was sampled from each tube once in October 2010, January and July 2011 using a 30 ml syringe. Samples were immediately transferred to a pre-evacuated 22 ml glass vial, over pressurised in the field but returned to lab pressure prior to analysis. Gas analysis was carried out using the GC. CH_4 was detected using FID to give ppm and peak area measurements. As many measurements were higher than the lab standard CH_4 concentrations of A (3.9 ppm), B (50.4 ppm) and C (20.3 ppm), additional standards of 0.1 % (1000 ppm), 1 % (10,000 ppm) and 10 % CH_4 (100,000 ppm) were used to calculate ppm from area measurements more accurately. Soil CH_4 percentages for underground gas samples were calculated directly from soil CH_4 concentrations in ppm.

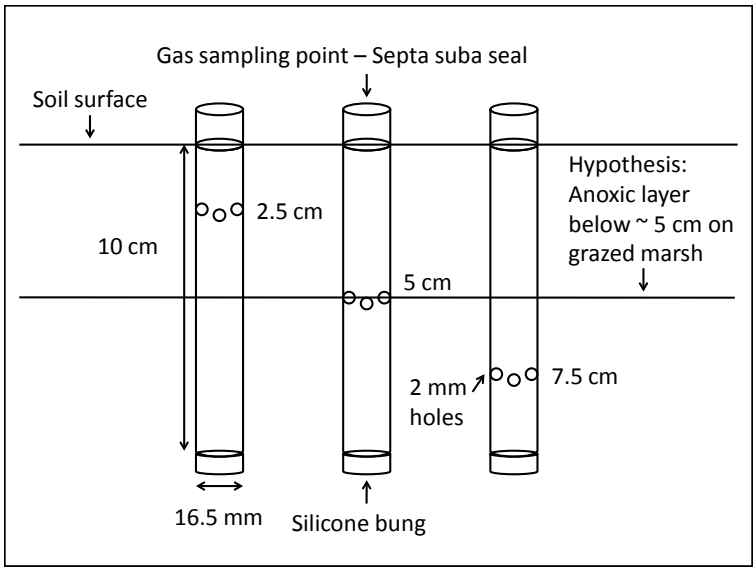

Figure 5.2 Schematic representation of the underground gas sampling tubes.

5.3.*6 Environmental measurements as predictors of chamber gas fluxes*

As soil temperature, soil moisture content and water table level are common drivers of soil greenhouse gas emissions these were measured monthly for twelve months alongside gas chamber measurements to provide possible predictive data for the size of greenhouse gas efflux. In addition plant community composition, particularly the presence of *Juncus* species, can influence the production of CH_4 via aerenchyma; this was therefore recorded in the middle of the twelve month sampling period and used in later predictive models (2.7). Soil temperature and soil moisture content were recorded adjacent to each chamber immediately prior to monthly gas measurements (with the same equipment as in section 2.2). It was also recorded if chambers or experimental units appeared waterlogged. Water table measurements were taken monthly at the same time as gas measurements from dip wells, one per experimental unit, located between the two chambers. The dip wells, 1 m depth, 35 mm internal diameter, PVC slotted screen (Stuart Well Services Ltd., Norfolk, UK), were installed in October 2010. Water table measurements were therefore not available for September or October. Plant species percentage cover was assessed by eye for each experimental unit during May 2011 for three 1 m x 1 m quadrats and within the two gas measurement collar areas.

5.3.7 Statistical analysis

Differences between grazing treatments for all environmental variables and flux measurements were analysed using ANOVAs on linear mixed effects (lme) models using R (R Development Core Team, 2011) taking into account the effect of sampling month 'lme (CO_2flux ~ grazing*month, random = ~1|block/grazing/month'. This approach was used to enable the raw data to be analysed accounting for replication at the level of the experimental unit (n=6; Crawley, 2007). In addition, lme models were used to assess the influence of water table level, soil moisture and soil temperature, all recorded alongside chamber measurements; percentage cover of *Agrostis stololinifera*, *Aster tripolium*, *E. repens*, *F. rubra*, *Glaux maritima*, *Juncus gerardii*, *Puccinellia maritima* and *Triglochin maritima* recorded from chambers and experimental units; and salinity,

bulk density, organic matter content, above ground biomass, litter biomass, all measured prior to chamber measurements; on underground soil CH_4 concentration and above-ground CO_2 and CH_4 fluxes. Results of best model fit are presented here based on lowest Akaike information criterion (AIC) and quantile probability plot (qqnorm) with most normal distribution.

5.3.8 Up-scaling conceptual diagram

A conceptual diagram was produced to compare the GWP of greenhouse gas fluxes from the grazed and un-grazed salt marsh over the Crossens marsh study site. Mean greenhouse gas fluxes from chamber measurements over the study year, for grazed versus un-grazed marsh (n = 6), were converted to CO_2 equivalents (g CO_2e m^{-2} yr^{-1}) for a 100 year GWP (CO_2 = 1, CH_4 = 25, N_2O = 298; Denman *et al*., 2007) and expressed as a comparative flux estimate for grazing type. Carbon stored in plant biomass for the grazed and un-grazed salt marsh, over one year, was calculated from mean ANPP for each treatment using a shoot carbon value of 42 % (unpublished data) to give a value in g C m^{-2} yr^{-1}. This was then converted to CO_2 equivalents in g CO_2 m^{-2} yr^{-1} using a conversion factor of x 3.67 (molar mass of CO_2 = 44, molar mass of C = 12, 44/12 = 3.67). CO_2 allocated to roots was not calculated. In addition to variables directly measured within this study, CH_4 efflux via cattle, enteric (i.e. microbial fermentation within rumen and large intestine), from waste and via trampling were also estimated to provide a more realistic comparison between grazing regimes. CH_4 efflux via cattle was calculated based on 100 bullocks on Crossens Marsh over 517 ha for 1/3 of the year (beef cattle emit 48 kg CH_4 hd^{-1} yr^{-1} enteric CH_4 & 6 kg CH_4 hd^{-1} yr^{-1} CH_4 from waste; IPCC 1996). CH_4 efflux via ebullition caused by cattle trampling was not directly measured but was included in the diagram as an additional factor that may influence greenhouse gas emissions as in (Herbst *et al*., 2011). The effect of grazing on GWP (CH_4 soil efflux + CH_4 cattle efflux + CO_2 efflux – ANPP = GWP (g $C0_2$e m^{-2} yr^{-1})) was analysed by ANOVA on an lme model using R as in section 2.7.

5.4 Results

5.4.1 Marsh characterisation

Bulk density, soil carbon stock, soil moisture content, soil temperature and below-ground plant biomass were all significantly higher on the grazed marsh in comparison to the un-grazed marsh. Soil pH, water infiltration rate, ANPP, above-ground plant biomass, litter biomass and vegetation height were all significantly greater on the un-grazed marsh (Table 5.1). Soil salinity and organic matter content were not significantly different between treatments although salinity showed greater spatial variability (between experimental units) on the grazed marsh. Nitrate mineralisation rate was significantly greater for the un-grazed marsh but ammonium mineralisation rate was significantly greater on the grazed marsh. Total nitrogen mineralisation was not significantly different between grazing treatments (Table 5.1). Below-ground meso-faunal feeding activity (Figure 5.3), a proxy for aerobic soil conditions, was significantly greater in un-grazed than grazed marsh (ANOVA; $F = 37.37$, d.f. = 5, $p < 0.01$). Within each marsh type feeding activity was faster in summer than autumn (ANOVA; $F = 18.89$, d.f. = 10, $p < 0.01$). On the grazed marsh no feeding activity was recorded below 4.5 cm in summer and 3 cm in the autumn, indicating possible anaerobic conditions.

5.4.2 CH_4 chamber fluxes

CH_4 fluxes were recorded monthly from September 2010 to August 2011 (Figure 5.4). Mean CH_4 fluxes fell within the range of 0.01 to 1.27 mg m^{-2} h^{-1} (GCflux model 2: linear flux, mean $r^2 = 0.68$). Peak CH_4 fluxes of up to 9.82 mg m^{-2} h^{-1} on the grazed marsh and 0.28 mg m^{-2} h^{-1} on the un-grazed marsh were recorded in February, one of the most water-logged months. CH_4 production showed high spatial heterogeneity between experimental units with chambers within G1 and G2 exhibiting consistently larger fluxes than other grazed units. There were no significant differences in CH_4 fluxes with grazing treatment, either for one year's data (Figure 5.4) or for each month separately but there were significant differences between months (ANOVA; $F = 3.22$, d.f. = 98, $p < 0.01$). For the grazed marsh soil moisture content and the presence of *J. gerardii* both positively increased CH_4 soil flux whereas increased temperature significantly decreased CH_4 flux (moisture ANOVA; $F = 6.73$, d.f. = 50, $p < 0.05$, Juncus ANOVA; $F = 14.34$, d.f. = 4, $p < 0.05$, temp ANOVA; $F = 8.10$, d.f. = 50, $p < 0.01$). For the un-grazed marsh no

soil or vegetation factors were significant for CH_4 flux, indicative of the negligible flux recorded for this treatment.

Table 5.1 Soil properties and vegetation characteristics measured from the grazed and un-grazed marsh. Sampling depths are presented alongside treatment means ± 95% confidence intervals, ANOVA results (n = 6) and number of replicate samples per experimental unit. For vegetation height, for each of the 6 replicates per treatment the mean of 10 measurements was used in the analysis. Org. mt indicates organic matter. This table includes some results previously published in Ford *et al*. (2012).

	Depth (cm)	Grazed	Un-grazed	F statistic		Rep
Soil						
Salinity (PSU)	0-15	2.5 ± 1.0	2.0 ± 0.7	1.78	*ns*	3
pH	0-15	7.6 ± 0.2	7.9 ± 0.2	7.49	*	3
Bulk density (g cm^{-3})	0-15	0.8 ± 0.1	0.7 ± 0.0	11.56	*	3
Organic matter content (%)	0-15	7.4 ± 1.5	6.3 ± 0.8	0.48	*ns*	3
Carbon stock (kg C m^{-2})	0-15	4.74 ± 0.7	3.69 ± 0.3	7.51	*	3
Moisture content (%)	0-6	52.6 ± 0.2	44.5 ± 2.5	10.32	*	6
Water infiltration rate (mm min^{-1})	n/a	0.02 ± 0.01	8.52 ± 2.06	182.98	** *	2
Temperature (^oC)	0-11	14.9 ± 0.1	14.2 ± 0.1	37.52	**	6
Nitrogen mineralisation rates						
NO_3^- (µg N g^{-1} dry wt day^{-1})	0-15	0.04 ± 0.03	0.25 ± 0.15	32.87	**	3
NH_4^+ (µg N g^{-1} dry wt day^{-1})	0-15	0.08 ± 0.03	0.02 ± 0.02	24.59	**	3
NO_3^- & NH_4^+ (µg N g^{-1} dry wt day^{-1})	0-15	0.12 ± 0.05	0.28 ± 0.15	2.50	*ns*	3
NO_3^- (µg N g^{-1} org. mt day^{-1})	0-15	0.54 ± 0.48	3.75 ± 2.16	52.37	** *	3
NH_4^+ (µg N g^{-1} org. mt day^{-1})	0-15	1.19 ± 0.57	0.34 ± 0.28	18.34	**	3
NO_3^- & NH_4^+ (µg N g^{-1} org. mt day^{-1})	0-15	1.73 ± 0.76	4.10 ± 2.21	5.56	*ns*	3
Vegetation						
Above-ground net primary productivity (kg dry wt m^{-2} yr^{-1})	n/a	0.58 ± 0.10	1.20 ± 0.16	9.09	*	3
Above-ground biomass (kg dry wt m^{-2})	n/a	0.3 ± 0.1	0.7 ± 0.1	24.15	**	5
Litter biomass (kg dry wt m^{-2})	n/a	0.0 ± 0.0	0.3 ± 0.1	24.68	**	5
Below-ground biomass (kg dry wt m^{-2})	0-10	3.4 ± 0.4	1.0 ± 0.2	73.86	** *	5
Vegetation height (cm)	n/a	8.2 ± 0.8	19.2 ± 1.4	103.28	** *	6

Significant differences between grazing treatments indicated by *(P < 0.05), **(P < 0.01) and ***(P < 0.001). Non significant results recorded as *ns* (P > 0.05).

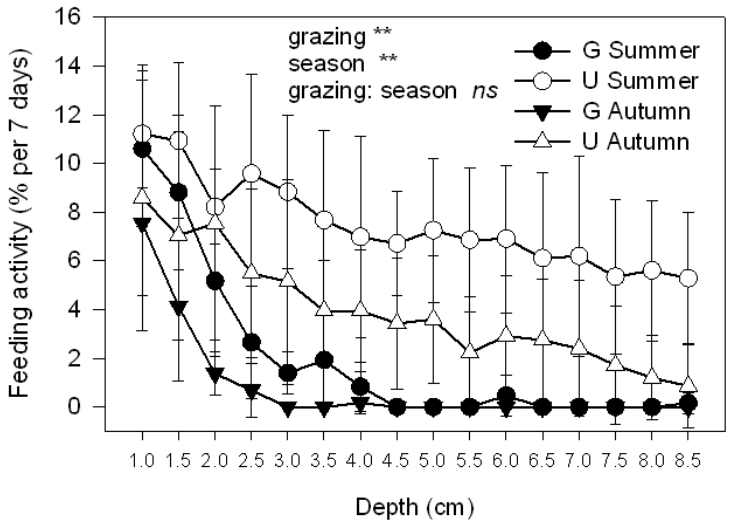

Figure 5.3 Below-ground meso-faunal bait lamina feeding activity for both grazing treatments (G = grazed; U = un-grazed) in summer and autumn 2009 as a function of soil depth. Values represent means ± 95% confidence intervals. Significant differences denoted by ** (P < 0.01), non-significant by *ns*.

5.4.3 CO_2 chamber fluxes

Mean monthly CO_2 fluxes of 74 to 949 mg m^{-2} h^{-1} were recorded, up to a peak of 2570 mg m^{-2} h^{-1} on the grazed and 1811 mg m^{-2} h^{-1} on the un-grazed marsh in June, one of the warmest months (GCflux model 2: linear flux, mean r^2 = 0.83). Grazing, month and grazing: month interaction all had significant effects on CO_2 fluxes (Figure 5.4) with warmer weather linked to larger fluxes, more often on the un-grazed than the grazed marsh (grazing ANOVA; F = 16.572, d.f. = 5, $p < 0.05$, month ANOVA; F = 22.68, d.f. = 110, $p < 0.001$, month:grazing ANOVA; F = 2.406, d.f. = 110, $p < 0.05$). High soil temperatures and deeper water table led to greater CO_2 fluxes for both grazing management treatments (temp ANOVA; F = 127.19, d.f. = 117, $p < 0.001$, water ANOVA; F = 14.885, d.f. 105, $p < 0.001$). For both the grazed and un-grazed salt marsh CO_2 fluxes were most spatially variable (between experimental units) over the summer months.

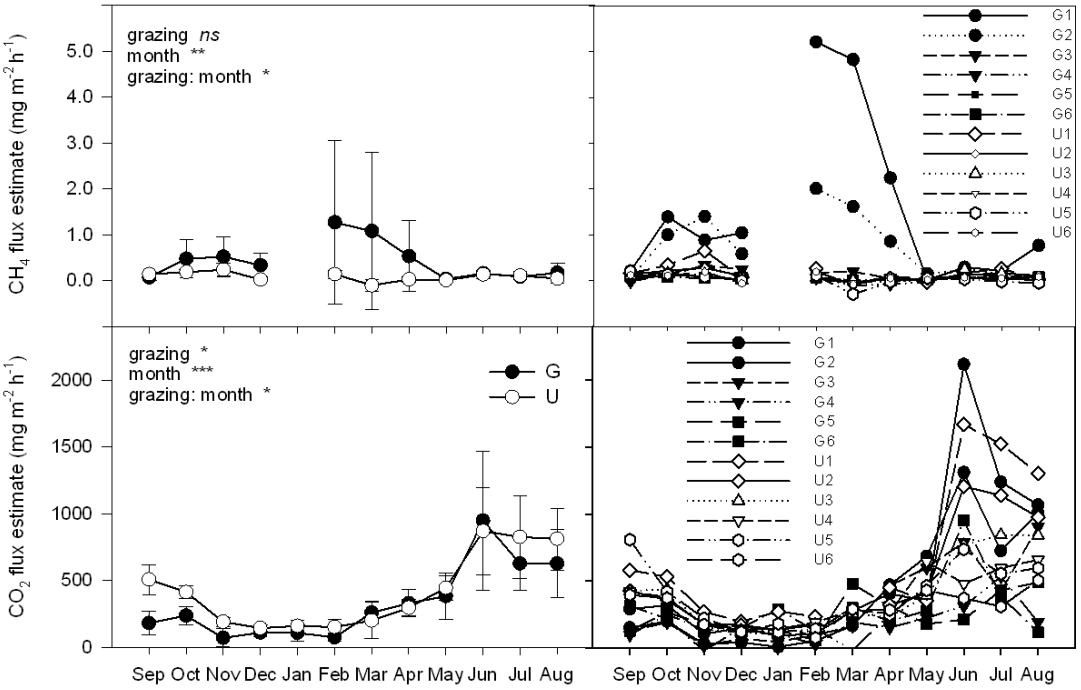

Figure 5.4 Monthly methane and carbon dioxide fluxes, comparison with grazing treatment (G = grazed; U = un-grazed) for September 10 to August 11. Values in left hand panels represent means ± 95% confidence intervals. Values in right hand panels represent mean of 2 gas chambers for grazed (G1-G6) and un-grazed (U1-U6) experimental units. Significant differences between grazing treatments, month or grazing: month interaction indicated by *(P < 0.05), **(P < 0.01) and *(P < 0.001). Non significant results recorded as *ns* (P > 0.05).**

5.4.4 N_2O chamber fluxes

N_2O fluxes of between -0.003 and 0.050 mg m^{-2} h^{-1} for the grazed and -0.040 and 0.005 mg m^{-2} h^{-1} for the un-grazed marsh were recorded over four months; September, November, December and January (model 2: linear flux, mean r^2 = 0.47); other months were excluded due to accidental moisture collection within vials leading to false peak area output on the GC. There were no significant differences in flux with grazing (ANOVA; F = 4.47, d.f. = 5, *ns*) and recorded fluxes were very low with a mean of 0.003 mg m^{-2} h^{-1}.

5.4.5. CH_4 soil concentration

During the waterlogged months of October and January, underground soil CH_4 concentrations were spatially variable (between experimental units), particularly on the grazed marsh, representing between 0.002 % and 6.29 % of the total soil air volume (Figure 5.5). In line with the results from the static chamber fluxes, the highest percentage of CH_4 was recorded from experimental units G1 and G2. The un-grazed marsh did not accumulate high levels of CH_4, 0.001 % to 0.081 %. CH_4 was only detectable in very low concentrations in July due to the very dry conditions. Underground soil CH_4 concentration was significantly different between time periods (month ANOVA; $F = 24.24$, d.f. = 22, $p < 0.001$) but not significantly different between grazing treatments. For the grazed salt marsh, lower soil temperatures and the presence of *J. gerardii* (saltmarsh rush) within units correlated significantly with soil CH_4 concentration (temp ANOVA; $F = 4.56$, d.f. = 35, $p < 0.05$, Juncus ANOVA; $F = 7.64$, d.f. = 4, $p < 0.05$). For the un-grazed salt marsh low soil temperatures and high soil moisture content correlated with high soil CH_4 concentration (temp ANOVA; $F = 89.210$, d.f. = 22, $p < 0.001$, Moisture ANOVA; $F = 4.618$, d.f. = 22, $p < 0.05$).

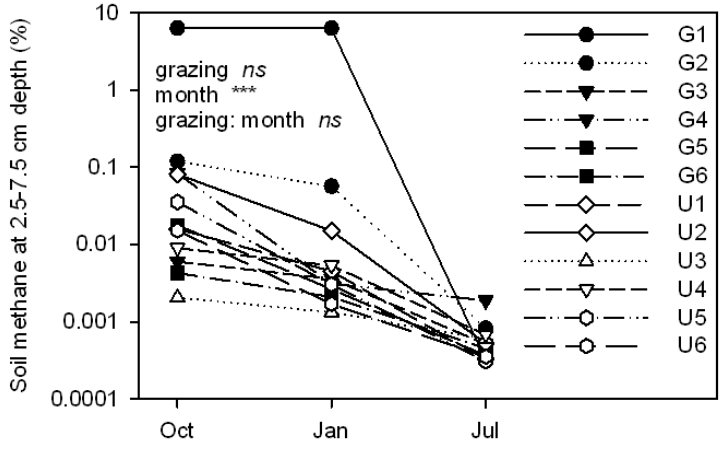

Figure 5.5 Influence of grazing on underground soil methane concentrations, expressed as percentage on a volumetric basis for October 2010, January and July 2011 on a log scale. Values shown for all grazed (G1-G6) and un-grazed (U1-U6) experimental units. Significant differences between grazing treatments, month or grazing: month interaction indicated by *(P < 0.001). Non significant results recorded as *ns* (P > 0.05).**

5.4.6 Environmental measurements as predictors of chamber gas fluxes

Soil temperature, measured adjacent to chambers, was significantly affected by grazing (ANOVA; $F = 8.08$, d.f. = 5, $p < 0.05$) and month (ANOVA; $F = 3962.765$, d.f. = 110, $p < 0.001$). As the interaction between grazing and month was also significant (ANOVA; $F = 19.931$, d.f. = 110, $p < 0.001$) this indicates that daytime soil temperature was higher on the grazed marsh during the spring and summer and higher on the un-grazed marsh in winter (Figure 5.6). Soil moisture adjacent to chambers, within the top 6 cm of soil, did not significantly alter with grazing (ANOVA; $F = 1.75$, d.f. = 5, *ns*) despite a trend towards higher moisture content in grazed soils in most months (Figure 5.6). The effect of month was significant (ANOVA; $F = 1.87$, d.f. = 98, $p < 0.05$). Water table level, measured within dipwells, was not significantly different between grazing treatments (ANOVA; $F = 0.02$, d.f. = 5, *ns*) but effect of sampling month was highly significant (ANOVA; $F = 57.99$, d.f. = 97, $p < 0.001$). Temperature, soil moisture, water table level and the presence of *J. gerardii* were all significant indicators of either CH_4 efflux, CO_2 efflux or soil CH_4 concentration as detailed in sections 3.2, 3.3 and 3.5.

5.4.7 Up-scaling conceptual diagram

The up-scaling conceptual diagram (Figure 5.7) shows no significant difference in GWP over 100 years for the grazed and un-grazed salt marsh (ANOVA; $F = 0.41$, d.f. = 5, *ns*). The GWP of the upper saltmarsh was estimated to be ~2000g CO_2e m^{-2} yr^{-1}, regardless of grazing management.

5.5 Discussion

5.5.1 Marsh characterisation

The grazed marsh was characterised, in 2009, by compact, moist soil, anaerobic below ~5 cm with high available ammonium characteristic of reduced conditions, probably caused by cattle trampling. Below ground root biomass and soil carbon stock were also greater on the grazed marsh. The un-grazed marsh had more aerobic, free draining soil, experienced a smaller range in temperature, with greater available nitrate and faster below-ground meso-faunal feeding rate than the grazed

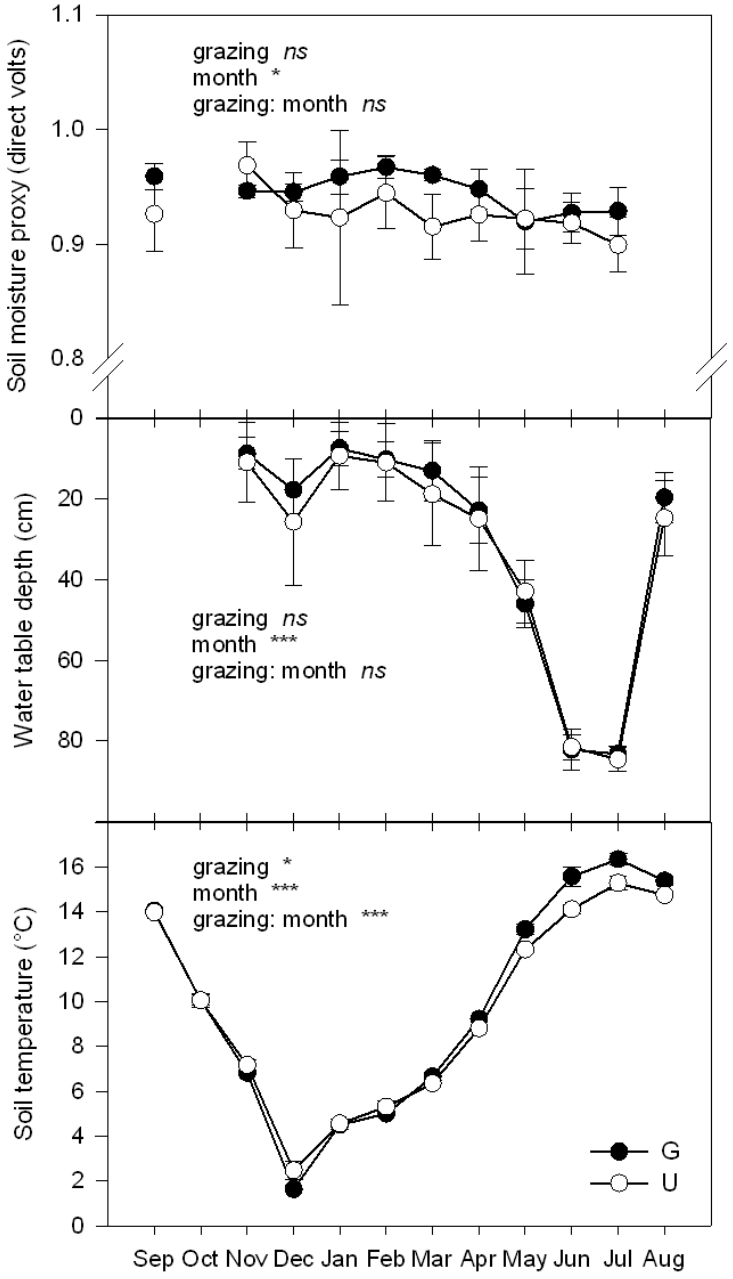

Figure 5.6 Influence of grazing on soil moisture, water table depth and soil temperature, measured monthly alongside gas measurements. Values represent means ± 95% confidence intervals. Significant differences between grazing treatments, month or grazing:month interaction indicated by *(P < 0.05), **(P < 0.01) and *(P < 0.001). Non significant results recorded as *ns* (P > 0.05).**

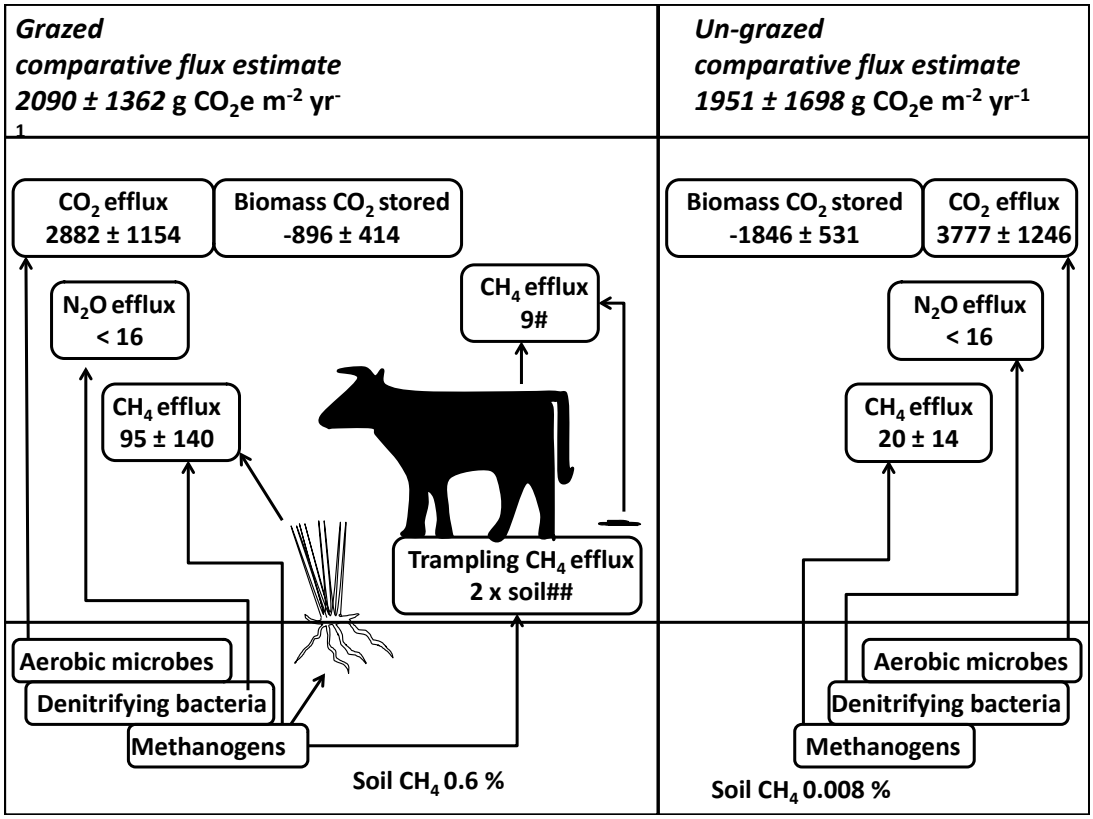

Figure 5.7 Up-scaled conceptual diagram for total greenhouse gas efflux from grazed and un-grazed salt marsh using yearly means (calculated from monthly means; Fig. 6.), ± 95% confidence intervals, to give a flux estimate per year for Crossens Marsh. All gas fluxes are expressed in g CO_2e m^{-2} yr^{-1} for Global Warming Potential (GWP) of 100 years (CO_2 = 1, CH_4 = 25, N_2O = 298; Denman *et al*., 2007). No significant difference in GWP between grazed and un-grazed salt marsh (ANOVA; F = 0.41, d.f. = 5, *ns*). # CH_4 efflux via cattle (calculated for Crossens Marsh; IPCC, 1996); ## CH_4 efflux via ebullition caused by cattle trampling (Herbst *et al*., 2011).

marsh. Grazing intensity also clearly affected vegetation characteristics, with the grazed marsh characterised by short vegetation and greater plant diversity. Fast growing dominant species such as *E. repens* were not present on the grazed marsh allowing rushes such as *J. gerardii* to develop, in comparison the un-grazed salt marsh was mainly a monoculture of *E. repens* with no *Juncus* species present. Above-ground plant and litter biomass were greater on the un-grazed marsh.

In addition to preliminary marsh characterisation the key known drivers of greenhouse gas emissions: soil temperature, soil moisture content, water table level and plant community were measured alongside chamber measurements for

the 2010-2011 experimental period. This allowed us to measure the effect of grazing and season on both environmental characteristics and greenhouse gas efflux. Results indicated that despite differences in temperature and soil moisture content between grazing treatments, the effect of month of measurement was a more important determinant of environmental characteristics than grazing treatment *per se*. For example, soil temperature spanned a range of ~15 °C over the measurement year but differences between grazing treatments were rarely greater than ~2 °C except in the summer months. Also, water table depth ranged from <30 cm over winter and spring to >80 cm in summer but remained constant across grazing treatments.

5.5.2 CH_4

Grazing intensity was not a significant predictor of either soil CH_4 concentration or CH_4 soil efflux. However, for the grazed salt marsh both under-ground and soil efflux CH_4 were spatially variable, with 'hotspots' occurring in conditions of high soil moisture content, low soil temperature and presence of *J. gerardii*. During the waterlogged autumn and winter months, underground soil CH_4 concentrations of up to 6 % and a peak CH4 flux of 9.82 mg m^{-2} h^{-1} were recorded from the grazed marsh. In contrast, the highest recorded soil CH_4 level from the un-grazed marsh was 0.08 %, with a peak flux of 0.28 mg m^{-2} h^{-1}. Over the one year study period, mean monthly CH_4 fluxes across both grazing treatments varied from 0.01 to 1.27 mg m^{-2} h^{-1} in line with fluxes recorded from North American and Australian salt marshes, a temperate tidal lagoon and a European flooded coastal meadow (Priemé, 1994; Deborde *et al*., 2010; Chmura *et al*., 2011; Livesley & Andrusiak, 2012) but greater than those recorded from a UK salt marsh (Dausse *et al*., 2012). Our variable soil CH_4 fluxes support the recent review by Poffenbarger *et al*. (2011), that oligohaline marshes have more temporally and spatially variable emissions than previously thought.

It is well known that CH_4 efflux is increased by anaerobic waterlogged soils (Ding *et al*., 2004; Kankaala *et al*., 2005). It is more unusual for soil CH_4 flux to be correlated with low temperatures, as in this study. In fact, high soil temperatures are usually

indicative of high CH_4 efflux (Le Mer & Roger, 2001). This unexpected result can be explained by high temperatures being correlated to drier summer months, where CH_4 flux was minimal or absent. The positive relationship between *Juncus* within plots and CH_4 flux may be due to *Juncus* itself, or the conditions it needs to grow. Roslev and King (1996) found that *Juncus effusus* stems, growing in a freshwater marsh, act as a conduit for CH_4 release from soil. In addition, the largest CH_4 efflux from a North American salt marsh was recorded from a mixed *Juncus* – *Carex* plant community (Magenheimer *et al*., 1996). Plant mediated CH_4 transport, via aerenchyma, may account for up to 90 % of total soil CH_4 efflux in vegetated marshes (Livingston & Hutchinson, 1995; Van der Nat & Middelburg, 1998; Van der Nat & Middelburg, 2000). Methanogens are usually most active at neutral or slightly alkaline conditions (Le Mer & Roger, 2001), as provided by both grazing treatments in this study. Soil organic matter content was not found to be indicative of CH_4 efflux in the study salt marsh. As peak CH_4 soil efflux was relatively low compared to the high CH_4 concentration found under the soil on the grazed upper salt marsh, it is likely that the majority of CH_4 produced is subsequently oxidised by methanotrophs at the soil surface or rhizosphere where oxic conditions exist (Ma & Lu, 2011). As livestock grazed salt marshes are often characterised by compact soil, prone to waterlogging, and the presence of *Juncus* species (Bakker *et al*., 1993; Lambert, 2000; Bos et al., 2002) it is possible that this management may increase soil CH_4 efflux.

5.5.3 CO_2

Grazing was a significant predictor of CO_2 efflux, with greater fluxes recorded from the un-grazed marsh throughout summer, autumn and winter but from the grazed marsh during spring. CO_2 efflux was of greater magnitude than the CH_4 efflux. With mean annual fluxes of 420 mg m^{-2} h^{-1} for un-grazed and 333 mg m^{-2} h^{-1} for the grazed marsh, up to a peak of 2570 mg m^{-2} h^{-1} in summer, these values are broadly comparable to both UK and North American salt marshes (Chmura *et al*., 2011; Dausse *et al*., 2012), and illustrate the importance of season to the magnitude of CO_2 flux. We can infer from biomass and ANPP measurements that above-ground carbon storage was greater in un-grazed salt marsh. In contrast, root and soil

carbon stocks were greater in the grazed marsh as in Allard *et al*. (2007). High rates of CO_2 efflux, from both grazing treatments, were positively predicted by a deeper water table, indicative of aerobic soil and higher soil temperatures as in Luo & Zhou (2006). Studies from grasslands, tidal flats and saltmarshes show that soil CO_2 efflux is consistently amplified by increasing soil or air temperature (Raich, 1992; Klassen & Spilmont, 2012). We therefore suggest that temperature fluctuation due to seasonal trends and future climate change are more important to the carbon budget of temperate salt marshes than grazing management.

5.5.4 N_2O

Grazing was not a significant predictor of N_2O soil emissions throughout the winter months. The grazed marsh had higher ammonium mineralisation rates but lower nitrate mineralisation rates than the un-grazed salt marsh. As nitrates are more readily converted to N_2O than ammonium it might be expected that the un-grazed marsh would produce more N_2O than the grazed marsh but this was not the case. Higher fluxes of N_2O, up to 0.05 mg m^{-2} h^{-1} were recorded from the grazed marsh, compared to a maximum of 0.005 mg m^{-2} h^{-1} from the un-grazed marsh. These results are comparable to cattle grazed and un-grazed New Zealand grassland (Saggar *et al*., 2007) but lower than values recorded for a UK saltmarsh (Blackwell *et al*., 2010). As the recorded fluxes were very low and not predicted by any measured soil or vegetation characteristics we regard the upper saltmarsh as neither a source nor sink of N_2O.

5.5.5 Validity of up-scaling

Static chambers are perhaps not the best way to measure overall greenhouse gas budgets for a habitat such as a saltmarsh due to temporal and spatial flux variations (Denman *et al*., 2007). However, they are an essential tool in the measurement of treatment differences such as grazing intensity that would be largely impossible with the eddy covariance technique (Sullivan *et al*., 2010), which is more applicable to catchment scale measurements. Within this study we provided a conceptual diagram (Figure 5.7) of mean comparative yearly flux estimates of GWP for grazed and un-grazed saltmarsh and found that grazing management does not significantly

alter GWP. This comparative approach was justified as sampling monthly for one year provided a fuller picture of soil greenhouse gas efflux than sampling just once or twice as was common in previous saltmarsh studies (Lindau & Delaune, 1991; Wang *et al*., 2007; Dausse *et al*., 2012). In order to make this up-scaling exercise more realistic, in addition to directly measured soil greenhouse gas emissions and ANPP, CH_4 efflux via cattle (enteric and waste) was also estimated based on cattle intensity at the study site. Cattle may also increase soil CH_4 efflux via trampling. Herbst *et al*. (2011) found that CH_4 flux doubled from background 'soil' levels when cows grazed in the vicinity of an eddy covariance tower, although part of this effect may be due to CH_4 released directly from the cows, it is also likely that part of this effect is CH_4 ebullition via trampling. This potential CH_4 source would be greatest when livestock were present on the salt marsh during waterlogged times of year. In this study CO_2 soil efflux was responsible for a much larger proportion of GWP than CH_4 efflux, only partially offset by the CO_2 'locked up' in plant biomass (Figure 5.7). The conditions needed for high rates of soil respiration, a low water table and warm soil, were the opposite of the cooler waterlogged soil conditions that stimulated soil CH_4 efflux. Where N_2O soil efflux was measured it did not contribute markedly to GWP. As GWPs for grazed and un-grazed saltmarsh were estimated from a combination of chamber measurements and ANPP it is not possible to directly compare the estimated GWP of ~2000 g CO_2e m^{-2} yr^{-1}, regardless of grazing intensity, to the GWP of other habitats. However this flux was of comparative magnitude to a North American peat land (Strack & Waddington, 2007).

5.6 Conclusion

In this study it was hypothesised that livestock grazing management would influence soil physical characteristics (e.g. soil temperature and moisture content) and plant community composition (e.g. presence of *Juncus* species) that would in turn regulate the CH_4, CO_2 and N_2O fluxes of saltmarsh habitats. Our results showed that soil temperature, soil moisture content, water table depth and the presence of *J. gerardii* were the most significant predictors of saltmarsh greenhouse gas flux. However, the effect of grazing intensity on these variables was small compared to the much greater impact of seasonal variability. Our first hypothesis

was refuted, as soil methane efflux was not consistently greater in the cattle grazed than the un-grazed salt marsh. However, 'hot spots' of both underground soil methane concentration and soil methane efflux were only present on the grazed marsh, occurring under conditions of high soil moisture content, low soil temperatures and the presence of *J. gerardii*. Our second hypothesis, that combined soil respiration and plant carbon dioxide efflux would be greater in the un-grazed marsh, was partially substantiated as CO_2 efflux was greater from the un-grazed marsh throughout the majority of the year and was positively correlated with deeper water table and higher soil temperatures. Our third hypothesis, that soil nitrous oxide efflux would be consistently greater from the grazed salt marsh was refuted due to lack of evidence. Grazing was not a significant predictor of N_2O soil emissions. The GWP (100 years) of a temperate upper salt marsh, calculated from mean yearly chamber fluxes of greenhouse gases (CH_4 and CO_2) and offset by ANPP, was not significantly altered by livestock grazing management.

5.7 Acknowledgements

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Chapter 6: Grazing effects on microbial community composition, growth and nutrient cycling in salt marsh and sand dune grasslands

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6.1 Abstract

The effect of grazing by large herbivores on the microbial community, and the ecosystem functions they provide is relatively unknown in grassland systems. Therefore, the impact of grazing upon the size, composition and activity of the soil microbial community was measured in field experiments established in two coastal grasslands: 'Grazed' (cattle grazed) and historically 'un-grazed' salt marsh; 'fully grazed' (ponies 0.2 ha^{-1}, cattle 0.05 ha^{-1} and rabbits 45 ha^{-1}), 'rabbit grazed' and 'un-grazed' (for 8 years) sand dune grassland. Total fatty acid phospholipids (PLFAs), bacterial and fungal PLFA concentrations, proxies for microbial biomass, were all significantly greater in grazed than un-grazed salt marsh ($p < 0.05$) and showed a trend towards greatest biomass in the rabbit grazed sand dune soil. Fungal-to-bacterial ratio did not differ with grazing for either habitat. Redundancy analysis (RDA) showed that soil moisture, bulk density and root biomass significantly explained the distribution of PLFA markers ($p < 0.05$) with a clear distinction between the saltmarsh and sand dune grassland habitats along axis 1 (89 %), driven by the soil moisture gradient. Grazing explained the separation of PLFA markers along axis 2 (7 %). Gram-positive bacteria and actinomycetes were more proportionally abundant in un-grazed, while Gram-negative bacteria dominated

more in grazed grasslands. Bacterial growth rate (Leucine incorporation) was greater in un-grazed salt marsh, possibly reflecting the more rapid nitrification rate, but did not differ with grazing in sand dune grassland. Grazing alters carbon (C) and nitrogen (N) soil inputs via changes in dung, plant litter, root exudates and root turnover rate. This in turn affects microbial biomass, composition and activity.

Keywords: Livestock grazing, decomposer ecology, bacterial growth rate, PLFAs, nutrient cycling

6.2 Introduction

Many types of semi-natural grasslands, including coastal grasslands, have been traditionally managed by low intensity cattle or sheep grazing. However, in the light of removal of European Union (EU) subsidies for marginal grazing land (Strijker, 2005; Taylor, 2006) it is not known how grazing abandonment will affect these habitats. The effects of large herbivore removal are relatively well studied for plant, invertebrate and bird communities (Morris, 2000; Vickery *et al*., 2001; Pykälä, 2003). However, effects upon the soil microbial community, and therefore soil ecosystem functions such as plant nutrient availability and organic matter decomposition, are less well known (Smith *et al*., 2003). Characteristic features of grazed and un-grazed grassland habitats are likely to have direct impacts upon soil microbial biomass, growth rates and community composition.

Cessation of livestock grazing leads to the gradual development of a plant community dominated by highly competitive tall grasses or shrubs with an increased plant litter layer (Bakker *et al*., 1993; Janišová *et al*., 2011) and has variable effects on root biomass, turnover and exudation (Piñeiro *et al*., 2010). Soil microbial activity and abundance are directly related to the quantity and quality of food sources such as plant litter, senescent roots and root exudates (Beare *et al*., 1991; Mawdsley & Bardgett, 1997; Grayston *et al*., 2001). Bacteria may benefit from higher quality litter with a lower C / N ratio and therefore a higher N nutrient

input. Grazing intensity also affects abiotic factors. Short grazed vegetation leads to greater and more variable soil temperatures than un-grazed grassland (Curry, 1994). Even a small increase in soil temperature may increase microbial activity and growth (Anderson, 1992) but is unlikely to affect community composition (Strickland & Rousk, 2010). Cattle compact the soil surface via treading leading to waterlogged ground (Lambert, 2000) and return nutrients to the soil via dung input (Bakker *et al*., 1993). Soil compaction will change soil structure and aeration with effects upon microbial community composition (Clegg, 2006). Grazing animals also return nutrients to the soil via dung input (Bakker *et al*., 1993) that greatly influences microbial activity in the soil. For instance, cattle faeces are a source of soil C and can increase microbial biomass and respiration (Lovell & Jarvis, 1996; Hatch *et al*., 2000) and livestock urine is a source of utilizable N linked to increases in respiration, nitrous oxide (N_2O) emissions and microbial biomass (Ritz *et al*., 2004).

Salt marshes differ from other terrestrial systems due to regular cycles of inundation by tides that transiently saturate the soil with water, and thereby limit oxygen availability. In these systems, the overriding influence of soil moisture (Waksman & Gerrettsen, 1931) is particularly emphasized. While microbial activity increases with higher water availability in dry conditions (Iovieno & Baath, 2008; Bapiri *et al*., 2010), the relationship changes at high water availabilities, and waterlogged soils exhibit reduced soil respiration (Luo & Zhou, 2006).

While it has been shown that factors including tillage (Six *et al*., 2006; Van Groeningen *et al*., 2010), N fertilization (de Vries *et al*., 2006) and grazing intensity (Bardgett *et al*., 2001; Klumpp *et al*., 2009; Lopez-Sangil *et al*., 2011) can affect the size and composition of the soil microbial community, the precise changes within the microbial community between different systems have not been addressed, and to date insights have been mostly limited to individual case-studies (Strickland & Rousk, 2010). For the microbial community, land-use factors are arbitrary, while

the direct influence of the micro-scale environment and growth conditions will be all important. That is, we will only be able to generalize effects of land-use to the extent that they expose microbial communities to selective pressures such as pH changes (Rousk *et al*., 2010) or organic matter quality (Rousk & Bååth, 2007).

In this study I investigated the impact of grazing intensity on the active soil decomposer community of temperate upper saltmarsh and fixed sand dune grasslands. These coastal grasslands are priority habitats under the Agri-Environment Scheme (Natural England, 2009). By including two independent grazing systems, we aimed to assess and relate the influence of grazing on the soil microbial community to the system specific differences inherent between ecosystems. Microbial biomass concentrations and community composition were measured using fatty acid phospholipids (PLFAs; Sundh *et al*., 1997) and bacterial growth rate by protein synthesis (Leucine incorporation; Kirchman *et al*., 1985). For the salt marsh two grazing treatments were used, 'grazed' (i.e. moderately cattle grazed) and 'un-grazed' (historically un-grazed). For the sand dune grassland three grazing treatments were used, 'fully grazed' (i.e. extensively cattle, pony and rabbit grazed), 'rabbit grazed' and 'un-grazed' (i.e. abandoned). We hypothesized the main source of variation in the microbial composition would occur between the two systems based on key environmental drivers such as soil moisture and nutrient availability, but that we would also find a secondary effect of grazing intensity.

6.3 Methods

6.3.1 Salt marsh

The study area, Crossens Marsh (53^{o} 41' 15" N, 2^{o} 57' 4" W), is a salt marsh located on the southern edge of the Ribble estuary in North-West England and is part of the Sefton Coast Special Protection Area managed by Natural England, the statutory conservation body. The marsh was historically un-grazed but was split into two management types over 40 years ago, un-grazed and cattle grazed by an

arbitrarily placed boundary fence. The grazed marsh is characterised by predominantly *Festuca rubra* saltmarsh NVC community (SM16d) and the un-grazed marsh by *Elytrigia repens* salt marsh (SM28; Rodwell, 2000). The grazed part of the marsh covers 517 ha and is uniformly grazed by around 100 bullocks from late May to early October, approximately 0.2 cattle (*Bos Taurus*) ha^{-1}, and provides a consistent short sward height (< 8 cm) for overwintering pink-footed geese (*Anser brachyrhynchus*) to feed. Small herbivores such as field voles are also present, particularly on the un-grazed marsh. All experimental units were selected within the high marsh zone where numerous creeks are present but tidal inundations are relatively rare, limited to around eight events a year on high equinox tides. A paired experimental design was used with six experimental units of approximately 10 m x 10 m set up on each side of a 600 m long section of the fence line, 100-150 m apart, in a 'mirror image' formation, giving six grazed (G1-G6) and six un-grazed (U1-U6) units (Figure 6.1). Each experimental unit was located between 20 m and 50 m from the fence line to ensure an adequate buffer zone and checked for standard elevation within ±10 cm. All measurements were carried out within these experimental units.

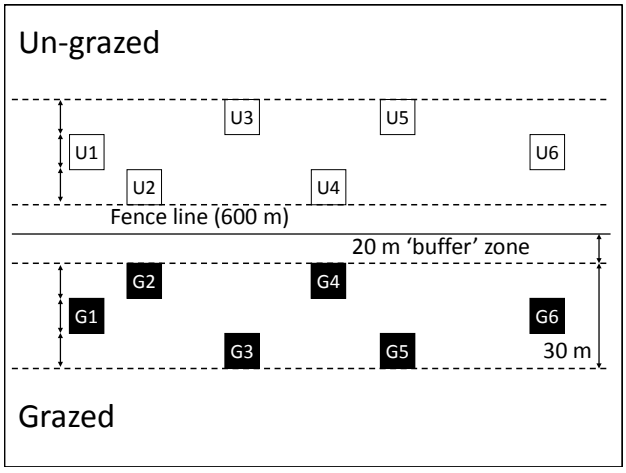

Figure 6.1 Experimental design at Crossens Marsh salt marsh, grazed experimental units (G1-G6) and un-grazed units (U1-U6). All units are 10 m x 10 m square at 20 - 30 m, 30 - 40 m or 40 - 50 m from the fence line. Not to scale.

6.3.2 Sand dune grassland

Newborough Warren is a calcareous coastal sand dune grassland, located in NW Wales (53° 8' 59" N, 4° 21' 1" W), noted for its high biodiversity and designated as a National Nature Reserve, Site of Special Scientific Interest and Special Area of Conservation under the EC Habitats and Species Directive 1992 (Plassmann *et al*., 2010). The 389 ha site is managed by Countryside Council for Wales (CCW) and grazed by Welsh mountain ponies (*Equus ferus caballus*; 0.2 ha^{-1}), rare breed cattle, Belted Galloways and Dexters (*Bos Taurus*; 0.05 ha^{-1}), and rabbits (*Oryctolagus cuniculus*; 45 ha^{-1}) (Plassmann *et al*., 2009), designed to maximise plant diversity. Grazed vegetation is characteristic of NVC SD12 and SD8 (Rodwell, 2000). In 2003, three replicate experimental units, each containing three 10 m x 10 m experimental, one fully grazed unit (unfenced), one rabbit grazed unit (fenced with 10 cm x 10 cm mesh to exclude large grazers) and one un-grazed unit (fenced with 10 cm x 10 cm mesh and an additional 2.7 cm x 3.7 cm mesh buried 20 cm underground to prevent rabbit access) were set up (Figure 6.2; Plassmann *et al*., 2009). Small mammals and invertebrate herbivores were assumed to be present within all experimental units. Fully grazed units are denoted as PR1 - PR3 (PR stands for pony & rabbit grazed); rabbit grazed units as R1 – R3 and un-grazed units as U1 - U3.

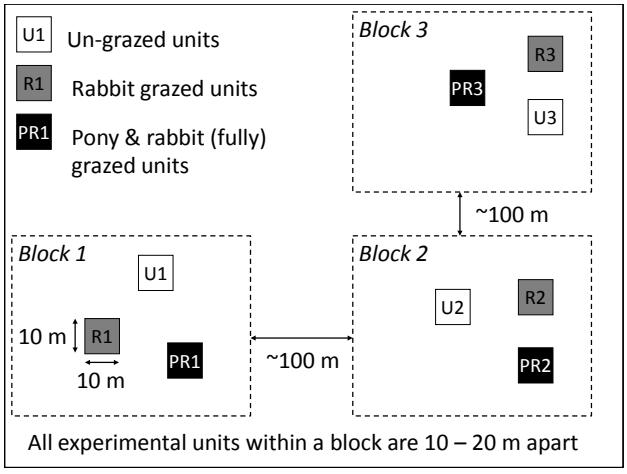

Figure 6.2 Experimental design at Newborough Warren sand dune grassland, three replicated blocks of three grazing treatments, fully grazed, rabbit grazed and un-grazed. Not to scale.

6.3.3 Soil and vegetation analyses

In November 2010, four soil cores (5 cm depth, 5 cm diameter) per experimental unit were taken, vegetation, roots and stones were removed and the remaining soil was sieved to ≤ 2 mm and stored for 1 week at 5 °C before further analyses. For soil respiration, 10 g sub-samples, four per experimental unit, were weighed into 50 ml polypropylene centrifugation vials and soil respiration rate at 22 °C measured continuously on a multichannel IR respirometer (PP-systems Ltd, Hitchin, UK). The reported soil respiration rate was the 4 hour average measurement taken after reaching a stable rate. Gravimetric soil moisture was estimated by determining the weight loss of samples dried initially at 105^{o}C for 72 hours. Subsequently, organic matter (OM) content was estimated by loss-on-ignition from soil sub samples (375 ^{o}C for 16 hours; Ball, 1964). Soil pH (5 g soil: 12.5ml water dilution factor) was determined using a Corning pH meter 220. Samples to determine bulk density were collected during September 2009 using three intact soil cores of 3.8 cm diameter and 15 cm depth from each experimental unit. Cores were dried at 105 ^{o}C for 72 hours and the dry mass divided by the volume of the core to calculate bulk density. Soil cores for total soil C and N were air dried, thoroughly homogenised and dried at 105 ^{o}C for 3 hours prior to analysis. Samples were analysed on an Elementar Vario-EL elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany), using oxidative combustion to detect C and N. The C / N ratio was also calculated using a weight ratio.

The potential for nutrient cycling by microbes was measured by N mineralisation. Three N mineralisation cores, 3.8 cm diameter and 15 cm depth, were taken from each experimental unit, during September 2009. Soil cores were taken using plastic corers, capped at both ends to minimise soil disruption, and stored intact at 4 °C. Accumulated inorganic N was flushed from the cores by spraying with a solution of similar ionic concentration to UK rain over 7 days until 150 ml of leachate had been

collected. Cores were incubated at 10 °C for 28 days, homogenised and a sub-sample extracted using 1 M KCl for the analysis of ammonium and nitrate content (Rowe *et al*., 2011). Mineralisable N was expressed as mg N g^{-1} OM (organic matter) for plant and microbial available N. Above-ground live vegetation (shoot) and plant litter were collected from five (two in sand dunes) 25 cm x 50 cm zones, cut to ground-level, in July 2009. One root core of 5 cm diameter and 10 cm depth was also taken per quadrat and washed to remove all soil. Above-ground vegetation, litter and roots were all dried at 80 °C for 24 hours and weighed to give indicators of above-ground shoot biomass, litter biomass and below-ground root biomass respectively. Root turnover was measured during September 2010 via four nylon 1 mm root turnover mesh strips (Normesh, UK), 2.5 cm wide x 15 cm long, placed in vertical cuts made in the soil with 2.5 cm overlap at the bottom and 2.5 cm emerging from the soil, 50 cm apart, across a 2 m transect in each unit. After 28 days the mesh strips were removed along with a slightly wider and deeper intact soil core. Cores were pushed out and divided in two along the mesh line, the number of fine roots penetrating each mesh depth zone (0 – 2.5 cm; 2.5 – 5 cm; 5 – 7.5 cm; 7.5 – 10 cm) were counted by eye as a proxy for fine root turnover (Lukac & Godbold, 2010).

6.3.4 PLFAs

The PLFA composition from a 1 g fresh soil sub-sample was determined according to Frostegård *et al*. (1993) with modifications (Nilsson *et al*., 2007). An internal standard (methyl nonadecanoate fatty acid 19:0) was added before the methylation step. To obtain indications of bacterial and fungal biomass specific PLFA markers were summed (Frostegård and Bååth 1996; Table 6.3). PLFAs were also grouped according to Gram-negative, Gram-positive bacteria and actinomycetes.

6.3.5 Bacterial growth rate and turnover times

Bacterial growth was estimated by measuring the incorporation of leucine (Leu) into bacteria (Kirchman *et al*., 1985) extracted from 1 g soil sub-samples (stored at 5 °C) using the homogenization / centrifugation technique (Bååth, 1994), with modifications (Bååth *et al*., 2001; Rousk & Bååth, 2011). We added 2 µl [^{3}H]Leu (37 MBq ml^{-1}, 5.74 TBq mmol^{-1}, Perkin Elmer) that was combined with non-labelled Leu, resulting in a final concentration of 275 nM Leu in the bacterial suspensions. The samples were then incubated for 2 h at 22 °C in the dark. Bacterial growth was estimated from the amount of Leu incorporated into extracted bacteria per hour and gram of soil. A rough index for bacterial turnover time was calculated by dividing the bacterial biomass (nmol PLFAs g^{-1}) by bacterial growth rate (nmol Leu incorporation g^{-1} h^{-1}).

6.3.6 Statistical analysis

Differences between pairs of grazing treatments (Salt marsh: G & U; Sand dune: PR & R, R & U, or PR & U) for all variables were analysed using linear mixed effects models (lme) in R v.2.12.1 (2010), e.g. lme (pH ~ grazing, random = ~1|block/grazing). This approach was used to enable the raw data to be analysed accounting for replication at the level of the experimental unit or block (Salt marsh n = 6; Sand dune n = 3). Where necessary, variables were log-, square root- or arcsine square root transformed. Results of best model fit are presented here based on lowest Akaike information criterion (AIC) number and quantile probability plot (qqnorm) with most normal distribution. For overall grazing effect, results are presented as an Analysis of Variance (ANOVA) of the lme model. For the sand dune data, significant differences between treatment pairs (e.g. PR & R) were reported directly from the lme analysis.

The relationship between salt marsh and sand dune grassland PLFA composition (mol-% of the 30 most abundant PLFAs; standardized to unit variance) and

environmental variables (soil parameters from Table 6.1 & 6.2) from grazed and un-grazed experimental units was analyzed with a redundancy analysis (RDA). RDA scaling was focused on inter-'species' (PLFAs) correlations and centered by species. Grazing treatment of each unit was included in the final RDA tri-plot but was not used to influence the analysis. The significance of environmental variables was tested using automatic forward selection (Monte Carlo test, 500 permutations). All multivariate analysis was carried out in Canoco v.4.5 (Ter Braak and Šmilauer, 2003). The RDA tri-plot shows a visual interpretation of the relationship between environmental variables and the distribution of PLFA markers for both salt marsh and sand dune grassland.

6.4 Results

6.4.1 Soil and vegetation characteristics

Organic matter content, bulk density, C/N ratio, net ammonification rate, root turnover and root biomass were all significantly greater on the grazed salt marsh grassland (Table 6.1). Net nitrification rate, soil pH, litter and shoot biomass were all significantly greater on the un-grazed salt marsh. Salt marsh soil basal respiration rate did not differ with grazing treatment. For the sand dune grassland, the majority of soil and vegetation variables did not differ significantly with grazing intensity (Table 6.2). Soil basal respiration rate and root biomass were greater in the fully and rabbit grazed than the un-grazed sand dune grassland. Litter biomass was greater in the rabbit and un-grazed than the fully grazed sand dune grassland. Net nitrification rate was greatest in the un-grazed sand dune soil.

Table 6.1 Soil and vegetation characteristics of the salt marsh in grazed and un-grazed experimental units (n = 6).

	Grazed	Un-grazed	Model SE	
Soil				
Organic matter content (%)	15.60	12.05	(1.16)	*
Basal respiration rate (µg C g^{-1} org. mt h^{-1})	23.92	23.35	(2.75)	*ns*
pH	7.15	8.07	(0.12)	***
Gravimetric soil moisture content (%)	126	111	(10.6)	*ns*
Bulk density (g cm^{-3})	0.81	0.72	(0.03)	*
C/N ratio	15:1	13:1	(0.55)	*
N mineralisation rate				
NO_3^- (µg N g^{-1} org. mt day^{-1})	0.54	3.75	(1.29)	***
NH_4^+ (µg N g^{-1} org. mt day^{-1})	1.19	0.34	(0.29)	**
Vegetation				
Root turnover (no. fine roots $month^{-1}$)	53.67	36.28	(3.98)	**
Root biomass (kg dry wt m^{-2})	3.37	0.96	(0.29)	***
Litter biomass (kg dry wt m^{-2})	0.01	0.34	(0.07)	*
Shoot biomass (kg dry wt m^{-2})	0.32	0.69	(0.07)	*

Treatment means and model standard error from linear mixed effects model (ANOVA) output
org. mt = organic matter
Significant differences between grazing treatments *($p < 0.05$), **($p < 0.01$) ***($p < 0.001$)
Non significant results *ns*

Table 6.2 Soil and vegetation characteristics of the coastal grassland for three grazing treatments (PR = fully grazed, R = rabbit grazed, U = un-grazed; n = 3).

	PR	R	U	Model SE	
Soil					
Organic matter content (%)	9.65	10.83	8.27	(0.96)	*ns*
Basal respiration rate (µg C g^{-1} org. mt h^{-1})	17.92 a	16.13 a	9.08 b	(2.31)	*
pH	6.21	6.16	6.01	(0.21)	*ns*
Gravimetric soil moisture content (%)	35.73	41.25	31.79	(3.73)	*ns*
Bulk density (g cm^{-3})	1.01	1.02	0.93	(0.04)	*ns*
C/N ratio	12:1	12:1	11:1	(0.31)	*ns*
N mineralisation rate					
NO_3^- (µg N g^{-1} org. mt day^{-1})	0.85 a	1.89	3.59 b	(0.91)	*
NH_4^+ (µg N g^{-1} org. mt day^{-1})	2.28	2.85	1.44	(1.00)	*ns*
Vegetation					
Root turnover (no. fine roots $month^{-1}$)	43.36 a	54.83 b	49.17 a	(3.84)	*
Root biomass (kg dry wt m^{-2})	1.24 a	1.22 a	0.71 b	(0.21)	*
Litter biomass (kg dry wt m^{-2})	0.12 a	0.22 b	0.28 b	(0.04)	*
Shoot biomass (kg dry wt m^{-2})	0.83	0.80	0.59	(0.20)	*ns*

Treatment means and model standard error from linear mixed effects model (ANOVA) output
org. mt = organic matter
Significant differences between grazing treatments (a is different from b) *($p < 0.05$), **($p < 0.01$)
Non significant results *ns*

6.4.2 PLFAs

Total PLFA, bacterial and fungal PLFA concentrations, proxies for microbial biomass, were all significantly greater in grazed than un-grazed salt marsh but did not differ with grazing treatment in sand dune soils (Figure 6.3). The relative abundances of both bacterial and fungal PLFA markers did not differ significantly with grazing treatment for either salt marsh or sand dune grassland; consequently the fungal-to-bacterial ratio did not differ between treatments (Tables 6.4 & 6.5). Gram-negative bacterial PLFAs were proportionally more abundant in the grazed, actinomycetes in the un-grazed salt-marsh soil. Gram-positive bacterial PLFAs were proportionally more abundant in the un-grazed than the fully grazed sand dune grassland.

Table 6.3 PLFA markers used for taxonomic groups.

Taxonomic group	PLFA group	Specific PLFA markers	Reference
PLFA biomarkers			
Bacteria	Multiple groups	i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7c, 10Me16:0, cy17:0, a17:0, 18:1ω7, cy19:0	Frostegård & Bååth, 1996
Gram-positive bacteria	Branched PLFAs	i15:0, a15:0, i16:0, i17:0, a17:0	O'Leary & Wilkinson, 1988
Gram-negative bacteria	Cyclopropyl and mono PLFAs	cy17:0, 16:1w7c, 16:1w7t and 18:1w7	Wilkinson, 1988
Actinomycetes	10Me-PLFAs	10Me16:0a, 10Me16:0b, 10Me17:0, 10Me 18:0	Kroppenstedt, 1985
Fungi	Polyunsaturated PLFAs	18:2ω6,9	Frostegård & Bååth, 1996
Fungal / bacterial ratio	Multiple groups	Fungi / Bacteria	Frostegård & Bååth, 1996

Table 6.4 Relative proportions of PLFA markers for grazed and un-grazed saltmarsh soil (n = 6).

	Grazed	Un-grazed	Model SE	
Bacteria (%)	60.2	59.7	(0.53)	*ns*
Fungi (%)	1.9	1.8	(0.23)	*ns*
Gram-positive bacteria (%)	15.4	15.9	(0.47)	*ns*
Gram-negative bacteria (%)	33.0	30.5	(0.85)	*
Actinomycetes (%)	6.4	8.2	(0.37)	**
Fungal/bacterial ratio	0.03	0.03	(0.01)	*ns*

Treatment means and model standard error from linear mixed effects model (ANOVA) output
Significant differences between grazing treatments *($p < 0.05$), **($p < 0.01$), non significant results *ns*

Table 6.5 Relative proportions of PLFA markers for sand dune grassland soil (PR = fully grazed, R = rabbit grazed, U = un-grazed; n = 3).

	PR	R	U	Model SE	
Bacteria (%)	52.2	51.2	53.2	(1.19)	*ns*
Fungi (%)	5.5	6.0	4.7	(0.01)	*ns*
Gram-positive bacteria (%)	16.4 a	15.3 a	19.2 b	(0.84)	*
Gram-negative bacteria (%)	25.6	25.9	23.0	(1.07)	*ns*
Actinomycetes (%)	8.9	8.8	10.1	(0.48)	*ns*
Fungal/bacterial ratio	0.11	0.12	0.09	(0.02)	*ns*

Treatment means and model standard error from linear mixed effects model (ANOVA) output
Significant differences between grazing treatments *($p < 0.05$), non significant results *ns*

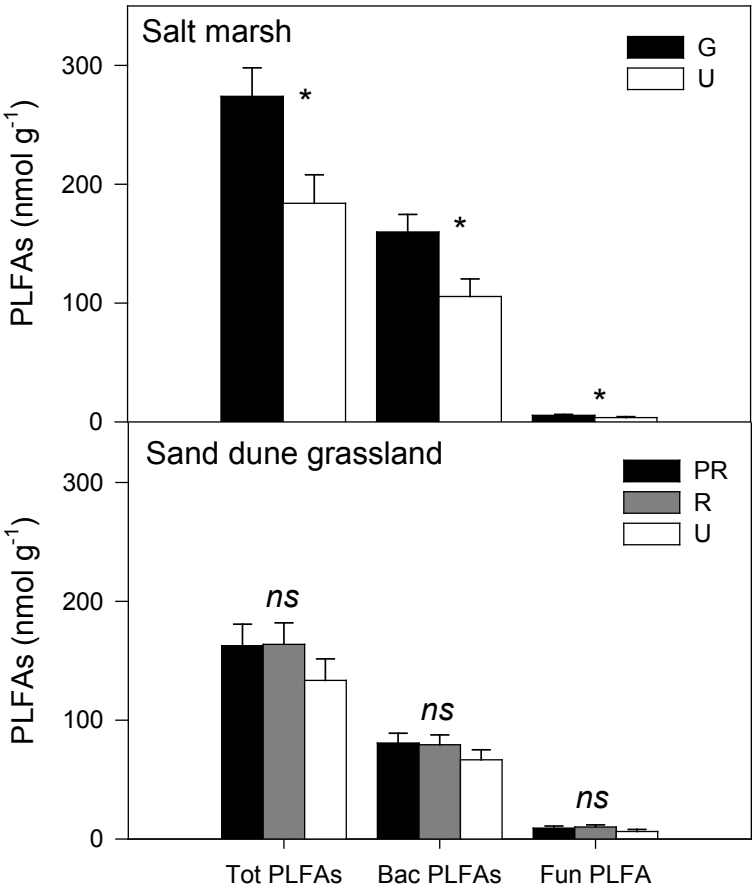

Figure 6.3 Total, bacterial and fungal PLFA concentrations for salt marsh (G = grazed; U = un-grazed) and sand dune grassland (PR = fully grazed; R = rabbit grazed; U = un-grazed). Treatment means and model standard error from linear mixed effects model (ANOVA) output. Significant differences between grazing treatments indicated by *($p < 0.05$), non significant results by *ns*.

6.4.3 PLFAs and environmental variables

The RDA tri-plot (Figure 6.4) shows the relationship between environmental variables and the distribution of PLFA markers for both salt marsh and sand dune grassland. Axis 1, and axes 1 and 2 combined, explained 89 % and 96 % of the variation in relative abundance of PLFA markers respectively. The Monte Carlo test for the first and all axes was significant for three environmental variables; gravimetric soil moisture (F-ratio = 48.86, $p < 0.01$), bulk density (F-ratio = 4.95, $p < 0.01$) and root biomass (F-ratio = 4.37, $p < 0.01$). All other environmental variables either correlated with these three or did not describe a significant proportion of PLFA marker occurrence. The RDA plot shows a clear distinction between the salt marsh and sand dune grassland habitats along axis 1, related to the soil moisture gradient. Grazing intensity, although not included within the analysis as an environmental variable, is related to separation of PLFA markers along axis 2. Un-grazed salt marsh and sand dune experimental units were all positively associated and grazed units negatively associated with axis 2. Using the PLFA markers composition to indicate how grazing intensity affected the microbial community composition we found that markers associated with Gram-positive bacteria (i.e. i17:0, i15:0) and actinomycetes (i.e. 10Me16:0a, 10Me 18:0) were relatively more abundant in soils with lower grazing pressures, while markers associated with Gram-negative bacteria i.e. (16:1w7t, 16:1w7c, 18:1w7) were relatively more abundant in systems with higher grazing pressures.

6.4.4 Bacterial growth rate and turnover times

Bacterial growth rate was significantly faster in un-grazed than grazed salt marsh, possibly reflecting the higher total soil N (Figure 6.5; Table 6.1). Bacterial growth rate was not significantly different between the sand dune grassland grazing treatments. The bacterial turnover time was also significantly quicker in un-grazed compared to the grazed salt marsh (ANOVA; $F = 16.99$, d.f. = 5, $p < 0.01$). Bacterial

turnover time did not differ significantly with grazing treatment for the sand dune grassland. Possible explanations of bacterial biomass, growth rate and turnover times in relation to nutrient cycling for the salt marsh and sand dune grasslands are proposed two conceptual diagrams (Figures 6.6 & 6.7).

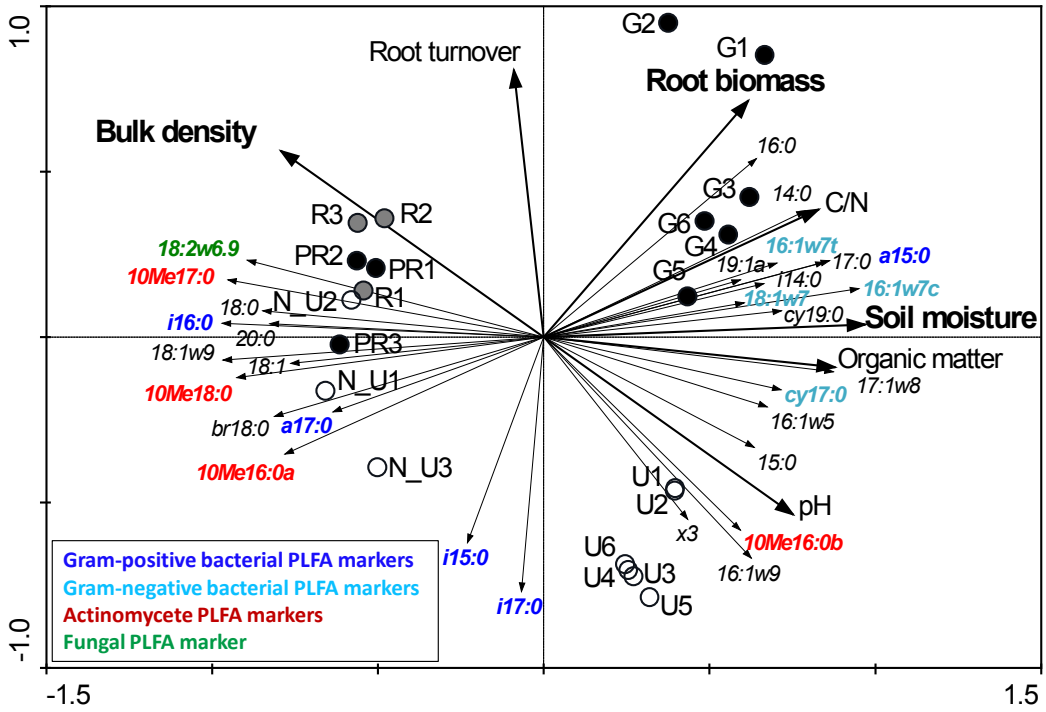

Figure 6.4 RDA triplot showing relationship between environmental variables and distribution of PLFA markers for both salt marsh and sand dune grassland experimental units (Salt marsh: G1-G6 = grazed, U1-U6 = un-grazed; Sand dune grassland: PR1-PR2 = fully, R1-R3 = rabbit grazed, N_U1-N_U3 = un-grazed; black circles = grazed or fully grazed, grey circles = rabbit grazed, white circles = un-grazed). Significant environmental variables (Canoco v.4.5; Monte Carlo test, 500 permutations) have larger, bold font.

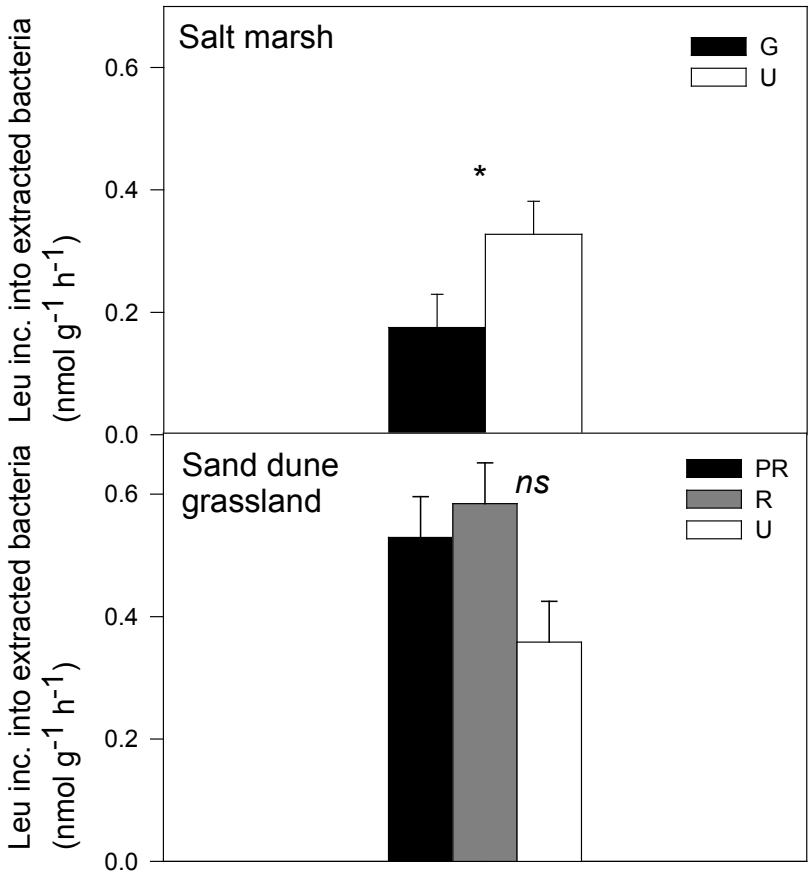

Figure 6.5 Bacterial growth rate for salt marsh (G = grazed; U = un-grazed) and sand dune grassland (PR = fully grazed; R = rabbit grazed; U = un-grazed). Treatment means, error bars as standard deviation of the mean. Significant differences between grazing treatments indicated by *($p < 0.05$), non significant results by *ns*.

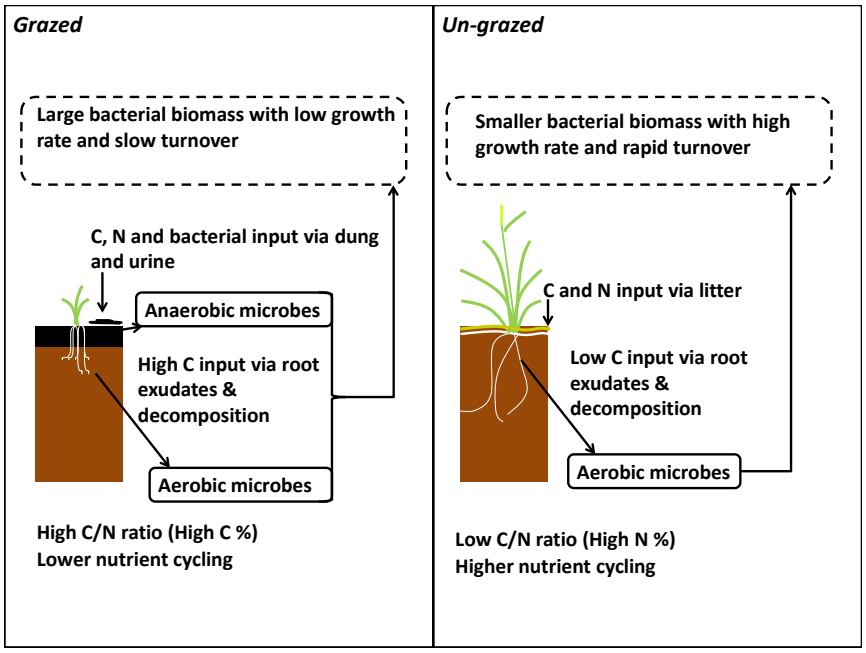

Figure 6.6 Conceptual diagram explaining differences in microbial biomass, activity and nutrient cycling between cattle grazed and un-grazed salt marsh.

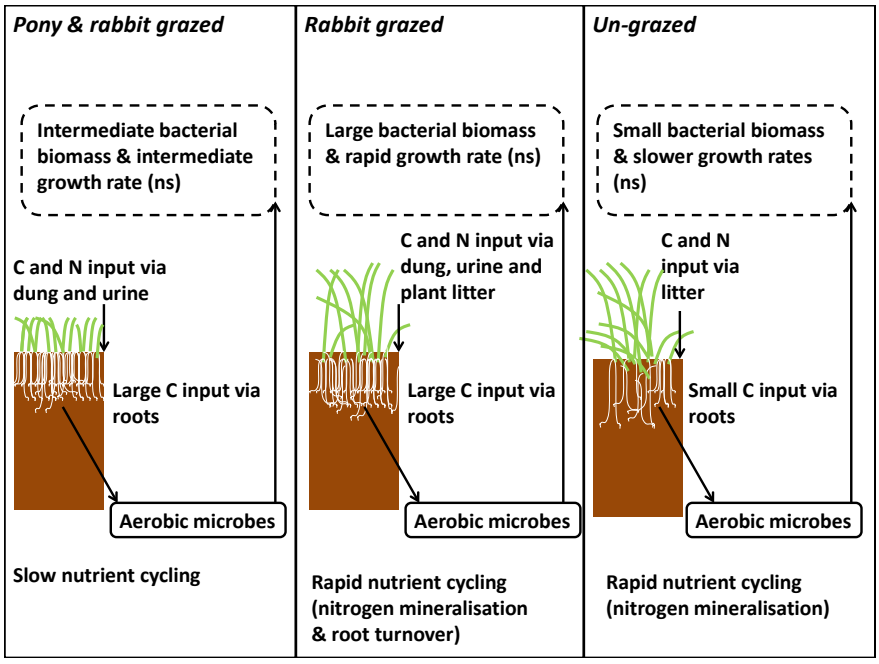

Figure 6.7 Conceptual diagram explaining differences in microbial biomass, activity and nutrient cycling for sand dune grassland grazing treatments (ns = non significant differences).

6.5 Discussion

6.5.1 Salt marsh microbial biomass, activity and nutrient cycling

In this study, saltmarsh microbial biomass was positively influenced by grazing as in other grassland soils (Bardgett *et al*., 1997; 2001) and was of a comparative magnitude to other salt marshes (Córdova-Kreylos *et al*., 2006). The fungal-to-bacterial balance was not altered by grazing intensity. Bacterial and fungal PLFA concentrations were both greater for grazed than un-grazed saltmarsh grassland, probably as a result of greater soil organic matter and C availability from dung input (Bardgett *et al*., 1998) and increased mycorrhizal fungi due to large root biomass and rapid root turnover rates. Paradoxically, despite the input of nutrient rich dung and urine into the grazed salt marsh soil the un-grazed salt marsh exhibited more rapid nutrient cycling in the form of greater N mineralization, possibly due to the greater plant litter input or better soil aeration. In addition, the un-grazed salt marsh soil exhibited a lower C / N ratio than the grazed marsh, indicative of high available soil N and potentially faster microbial cycling. This may explain the fact that both bacterial growth rate and estimated bacterial turnover times were faster in un-grazed than grazed salt marsh. It is often assumed that there is a direct positive relationship between bacterial growth rate and respiration rate. However, in this study the saltmarsh soil basal respiration rate did not differ with grazing treatment showing that this assumed relationship can be uncoupled (Iovieno & Bååth, 2008). Aerated lab samples may have artificially increased soil respiration recorded from the grazed salt marsh compared to true field conditions where the grazed marsh is often waterlogged and anaerobic (Chapter 5). An explanation of grazing effects on saltmarsh bacterial biomass, activity and nutrient cycling is illustrated in Figure 6.6.

6.5.2 Sand dune microbial biomass, activity and nutrient cycling

Total microbial biomass for our sand dune grassland soil was comparable to similar habitats (Chang *et al*., 2011). Bacterial and fungal PLFA concentrations did not differ significantly between fully, rabbit or un-grazed sand dune grassland. The fungal-to-bacterial ratio was also un-altered by grazing intensity. Bacterial growth rate and turnover time did not differ significantly with grazing treatment in this habitat, however a possible trend towards a more rapid growth rate in the rabbit grazed grassland was identified. The rabbit grazed or un-grazed (except by small mammals) soils exhibited more rapid nutrient cycling in the form of greater N mineralization, possibly due to the greater input of plant litter and more even distribution of small droppings. Soil organic matter content and root turnover rates were also greatest in the rabbit grazed habitat. Soil respiration rate was significantly greater in the fully and rabbit grazed sand dune grassland than the un-grazed grassland tentatively mirroring bacterial growth rate patterns. An explanation of grazing effects on sand dune grassland bacterial biomass, activity and nutrient cycling is illustrated in Figure 6.7.

6.5.3 Microbial composition patterns

Most of the variation, 89 % of the microbial PLFA composition, was related to site differences, clearly separating the salt marsh and sand dune communities on a soil moisture gradient. A smaller proportion of the total variation, 7 %, was consistently related to grazing intensity for both habitats and was partly explained by measured environmental variables including bulk density and root biomass. Using the PLFA markers composition to indicate how grazing intensity affected the microbial community composition we found that markers associated with Gram-positive bacteria and actinomycetes were relatively more abundant in soils with lower grazing pressures, while markers associated with Gram-negative bacteria were relatively more abundant in systems with higher grazing pressures.

Gram-positive bacteria may be aerobic or anaerobic (Paul & Clark, 1996), consequently it is difficult to assign this group a definite soil function. There is some evidence that they are fast growing (Bardgett *et al*., 1999) and are more reliant upon a C supply dominated by the soil organic matter from plant litter rather than the labile plant root exudates (Treonis *et al*., 2004; Olsson & Johnson, 2005; Bird *et al*., 2011). Actinomycetes are chemorganotrophic, filamentous bacteria (Paul & Clark, 1996). ~90% of soil actinomycetes are *Streptomyce*, capable of rapidly degrading less readily decomposable soil organic matter components (Tate, 2000), more common in un-grazed plant litter (Valery *et al*., 2004; Vargas Gil *et al*., 2009). Actinomycetes are adapted to water stress by resisting plasmolysis (Killham, 1994), allowing them to thrive in the un-grazed dry sand dune grassland. Actinomycete biomarkers are also common in unsaturated salt marsh sediment (Córdova-Kreylos *et al*., 2006).

Gram-negative bacteria, from our results proportionally more abundant in grazed grasslands, form close associations with the plant rhizosphere (Söderberg *et al*., 2004; Wardle *et al*., 2004), correlated with the presence of labile C resources, a result common to many habitats (Steer & Harris, 2000; Bird *et al*., 2011). Considering other PLFA markers, a denitrification marker, cy19:0 (Jackson *et al*., 2003), was very closely correlated with high soil moisture content and therefore occurred most frequently on the grazed salt marsh. An anaerobic bacterial marker, 16:0 (Findlay *et al*., 1990), was also characteristic of grazed plots. A greater relative abundance of monounsaturated fatty acids and the aerobic bacterial marker 18:1w9 (Findlay *et al*., 1990) on the un-grazed compared to the grazed marsh was indicative of more aerobic conditions.

6.6 Conclusions

This study explored the impact of grazing management on two coastal grassland soil microbial communities. Bacterial biomass was greatest in cattle grazed salt

marsh and rabbit grazed sand dune grassland, potentially due to the presence of a large root biomass, sometimes associated with rapid root turnover and a ready source of C from both root degradation and dung. Bacterial activity (growth rates and turnover times) was most rapid in un-grazed salt marsh and rabbit grazed sand dune grassland. Un-grazed salt marsh grassland had a much greater nitrification rate and potential decomposition rate than the grazed marsh due to potentially more aerobic soil conditions and the input of plant litter. Rabbit grazed sand dune grassland also had rapid nutrient cycling and C and N inputs from dung, urine and plant litter combined. These features explain the greater bacterial activity in un-grazed or rabbit grazed soils. Higher grazing intensity across both grassland habitats stimulated PLFA markers associated with Gram-negative bacteria, associated with the use of labile C resources from root exudates, while lower grazing intensity favoured a dominance of Gram-positive bacteria and actinomycetes, more dependent on the decomposition of plant litter. This study is an early step in assessing the consequences of land-use change on nutrient cycling driven by the soil microbial community.

6.7 Acknowledgements

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Chapter 7: Thesis discussion

Hilary Ford

7.1 Overview

In this thesis I have studied biodiversity, ecosystem function and ecosystem service provision in saltmarsh and sand dune grasslands. Firstly in the form of a literature review (Chapter 2) and secondly via four experimental research papers (Chapters 3–6) assessing the effect of land – use change via grazing introduction or grazing abandonment. It is clear from Chapter 3 that sand dune grassland grazing management involves trade-offs between the potential for ecosystem service provision provided by grasslands with different grazing intensities. Extensively cattle & pony grazed grassland was important for food provision, cultural environmental appreciation and potential pollination services, un-grazed or 'abandoned' grassland for potential pest regulation and nutrient cycling, rabbit grazed for a balance between the two. Chapter 6 provided a more in depth look at the soil microbial community composition in relation to the supporting service of nutrient cycling.

So far in this thesis the evidence for ecosystem service provision by cattle grazed and un-grazed saltmarsh grasslands has not been discussed. Evidence from the saltmarsh invertebrate paper (chapter 4) could be used to generate hypotheses concerning provision of food for wetland birds. For example, as large bodied invertebrates are more abundant on the un-grazed marsh and large detritivores an important food source for birds such as the endangered redshank (*Tringa tetanus*),

this habitat may offer greater availability of food for wetland birds than grazed salt marshes. Provision of habitat for wetland birds is of conservation interest and links to the cultural services of bird watching and wildfowling. In addition, the greater abundance of predatory spiders on the grazed marsh and in contrast, the greater abundance of predatory Coleoptera on the un-grazed marsh may have implications for the regulating service of pest control, especially where salt marshes border agricultural crop land, although at present this is untested and therefore speculative. The saltmarsh greenhouse gas balance chapter links directly to the regulating service of 'equable climate'. Chapter 6 also provides information on the relationship between the soil microbial community and nutrient cycling for salt marsh grasslands.

In order to assess how sand dune and saltmarsh grassland grazing management compare in the potential provision of ecosystem services evidence from chapters 3 (sand dune), 4 & 5 (salt marsh) and 6 (both habitats) have been combined, alongside supplementary data from the salt marsh analysed and presented in Table A7.1 and Figure A7.1. Two conceptual diagrams were created to compare the effect of livestock grazing on two contrasting coastal ecosystems, the 'high productivity – low biodiversity' salt marsh grassland and the 'low productivity – high biodiversity' sand dune grassland (Figure 7.1a & 7.1b). Salt marsh and sand dune grasslands provide many ecosystem services; environmental appreciation (cultural service), primary productivity and nutrient cycling (supporting services), pest control, pollination, equable climate, flood prevention or water storage (regulating services), and food production (provisioning service). Many of these overlap with services provided by semi-natural grasslands. Despite the differences in biodiversity, productivity and soil moisture content between the two experimental coastal grasslands, salt marshes and sand dunes, it is remarkable how similarly they react to the presence of large herbivore grazers in terms of potential ecosystem service provision (Figure 7.1). Grazing by large herbivores has two main ecosystem effects; a decrease in vegetation height and an increase in soil compaction. These in turn influence other ecosystem characteristics and functions that affect final ecosystem service provision.

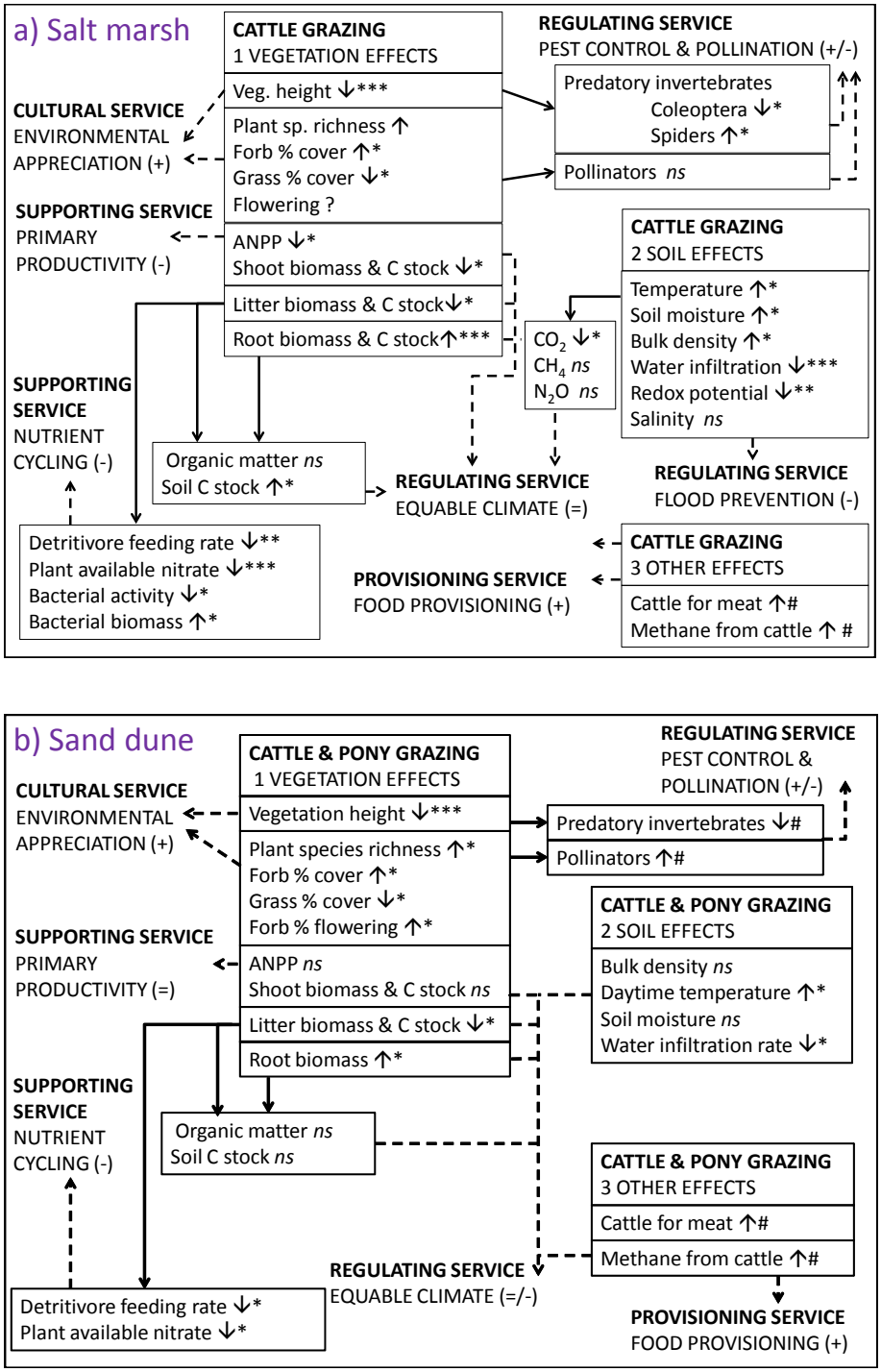

Figure 7.1 Effects of saltmarsh cattle grazing (a) and sand dune coastal grassland cattle and pony grazing (b) on vegetation, soil and other measured ecosystem characteristics as proxies for ecosystem service delivery. Measured ecosystem characteristics are shown in italics with a significant increase or decrease indicated by arrows (*p < 0.05, **p < 0.1, ***p < 0.001, *ns* p > 0.05) with grazer removal indicated by arrows, # for expected results from the literature. Solid lines show direct effects between variables, dashed lines show indirect effects to ecosystem services with positive, equal or negative effects indicated within brackets.

Reduced vegetation height favours an increase in species richness as dominant tall grasses are reduced and percentage cover of forbs and flowering of forbs increases. These factors infer an enhanced aesthetic environmental appreciation or 'cultural service'. Short grazed vegetation supports more small spiders but fewer large predatory Coleoptera than longer un-grazed vegetation, with variable effects on potential pest control, a 'regulating service' and possible implications for food provision for birds. For primary productivity and nutrient cycling, 'supporting services', the trend is towards reduced service provision for grazed grasslands due to decreased above ground net primary productivity (ANPP), detritivore feeding rate and plant and microbial available nitrogen. Large herbivore soil compaction leads to increased soil moisture content, reduced water infiltration rate and reduced aerobicity of the soil leading to a negative effect on flood prevention, a 'regulating service'. For equable climate, another 'regulating service', grazing has mixed effects. Root and soil carbon storage increases with grazing, a positive effect. But methane efflux from soil, via grazed salt marsh 'hotspots', and via cattle is also increased, a negative effect. Finally direct food production, a 'provisioning service', is only provided by livestock grazed coastal grasslands.

7.2 Conclusion

Extensive grazing management is often recommended for conservation of coastal grasslands as it maximises plant diversity and provides a suitable breeding habitat for particular bird species. In the light of abandonment of marginal grazing land throughout Europe, including salt marsh and sand dune grasslands, we suggest that in addition to biodiversity measures of 'success' in conservation, ecosystem service trade-offs need to be taken into account when choosing an appropriate grassland management scheme. Extensively or moderately cattle grazed coastal grasslands should be conserved for food provision, cultural environmental appreciation and pollination services, un-grazed grassland for flood prevention, pest regulation, primary productivity and nutrient cycling. The impact of grazing on equable climate, across different coastal grasslands, is not clear. This thesis conclusion highlights the fact that comprehensive measurement of management effects on both biodiversity

and ecosystem service provision needs to take place to inform a 'best compromise' for managers of all coastal and terrestrial habitats.

7.3 Future research questions

- What are the trade-offs in management for biodiversity and ecosystem service provision in other habitats?
- What are the biodiversity and ecosystem service benefits of *Elytrigia repens* un-grazed salt marshes? Are they always 'bad' for conservation as often assumed by conservation management bodies such as Natural England and RSPB?
- Large bodied invertebrates appear to be more abundant in un-grazed *Elytrigia repens* saltmarsh than conservation grazed marsh. What implications does this have for food provision for birds such as the redshank?
- Do other grazed saltmarshes experience methane hotspots linked to waterlogged soil and presence of *Juncus* species? Do saltmarsh creeks emit methane? What are the implications for greenhouse gas balance management?

7.4 Appendix

Table A7.1 Soil properties and vegetation characteristics measured from the grazed and un-grazed salt marsh (Crossens Marsh; Figure 4.2). Treatment means, lme model SE and ANOVA results (n = 6) are presented as in chapter 4. Nectar feeders were analysed with paired t tests in Genstat.

	Grazed	Un-grazed	Model SE	
Vegetation				
ANPP (kg dry wt m^{-2} yr^{-1})	0.58	1.20	0.20	*
Graminoid species richness	3.40	1.97	0.24	**
Forb species richness	3.17	1.73	0.59	*
Forb percentage	11.63	3.45	3.06	*
C stock				
Shoot C stock (t C ha^{-1})	1.36	2.90	0.28	**
Litter C stock (t C ha^{-1})	0.04	1.43	0.28	**
Root C stock (t C ha^{-1})	14.82	4.24	1.27	***
Total C stock (above & soil C stock) (t C ha^{-1})	63.98	45.14	4.52	**
Nectar feeders (pollinators)				
Abundance	72.17	84.67	11.03	*ns*
Species richness	9.00	8.17	0.95	*ns*

Significant differences between grazing treatments indicated by *($p < 0.05$), **($p < 0.01$) and ***($p < 0.001$). Non significant results recorded as *ns* ($p > 0.05$).

7.4.1 Methods for Table A7.1

7.4.1.1 Vegetation

Above ground net primary productivity (ANPP), peak biomass from three grazer excluded areas per experimental unit, was recorded as a direct measure of primary productivity. During early March 2009, vegetation was cut to ground level in three 50 cm x 50 cm areas per experimental unit. Each cut area was protected from pony, cattle and rabbit grazers by an 8 cm mesh gabion (50 x 50 x 50 cm) and vegetation allowed to re-grow until peak biomass at the end of August when areas were re-cut within a central 25 cm x 25 cm area. Vegetation was dried at 80 °C for 72 hours then weighed and converted to kg dry wt m^{-2} yr^{-1} to provide a measure of ANPP. Plant percentage cover and species richness were recorded by eye during July in five 1 m x 1 m quadrats from each experimental unit.

7.4.1.2 C stock

Carbon stock measurements (t C ha^{-1}) were derived from soil or biomass measurements (Chapter 4; section 4.3.3) for four pools: soil, roots, plant litter and

shoots, using the following conversions; Soil carbon is 0.55 of soil organic matter (Emmett *et al*., 2010); Root carbon is 0.44 of root biomass (dry wt) and plant litter and shoot carbon are 0.42 of biomass (dry wt) in grassland habitats (Jones *et al*., 2002; Jones *et al*., 2005).

7.4.1.3 Nectar feeders (pollinators)

Pollination was indirectly quantified by pan trap sampling of nectar feeders. Six baitless pan traps of three colours (2 blue, 2 white, 2 yellow) to attract nectar feeders were set for 72 hours during June and again in July 2009. In each experimental unit two triangles, 5 m apart, consisting of one pan trap of each colour, 1.5 m apart, was set up. Traps of the same colour were pooled to give three samples per experimental unit. Each trap consisted of 203 mm diameter bulb bowls sprayed yellow, blue or white, half filled with water containing a drop of washing up liquid to break the surface tension. Wire baskets of 5 cm mesh size were placed over all traps to prevent damage by grazing animals. The contents of the pitfalls and pan traps were preserved in 70 % Industrial strength methylated spirits (IMS) or ethanol and nectar feeders as potential pollinators were identified.

7.4.1.4 References

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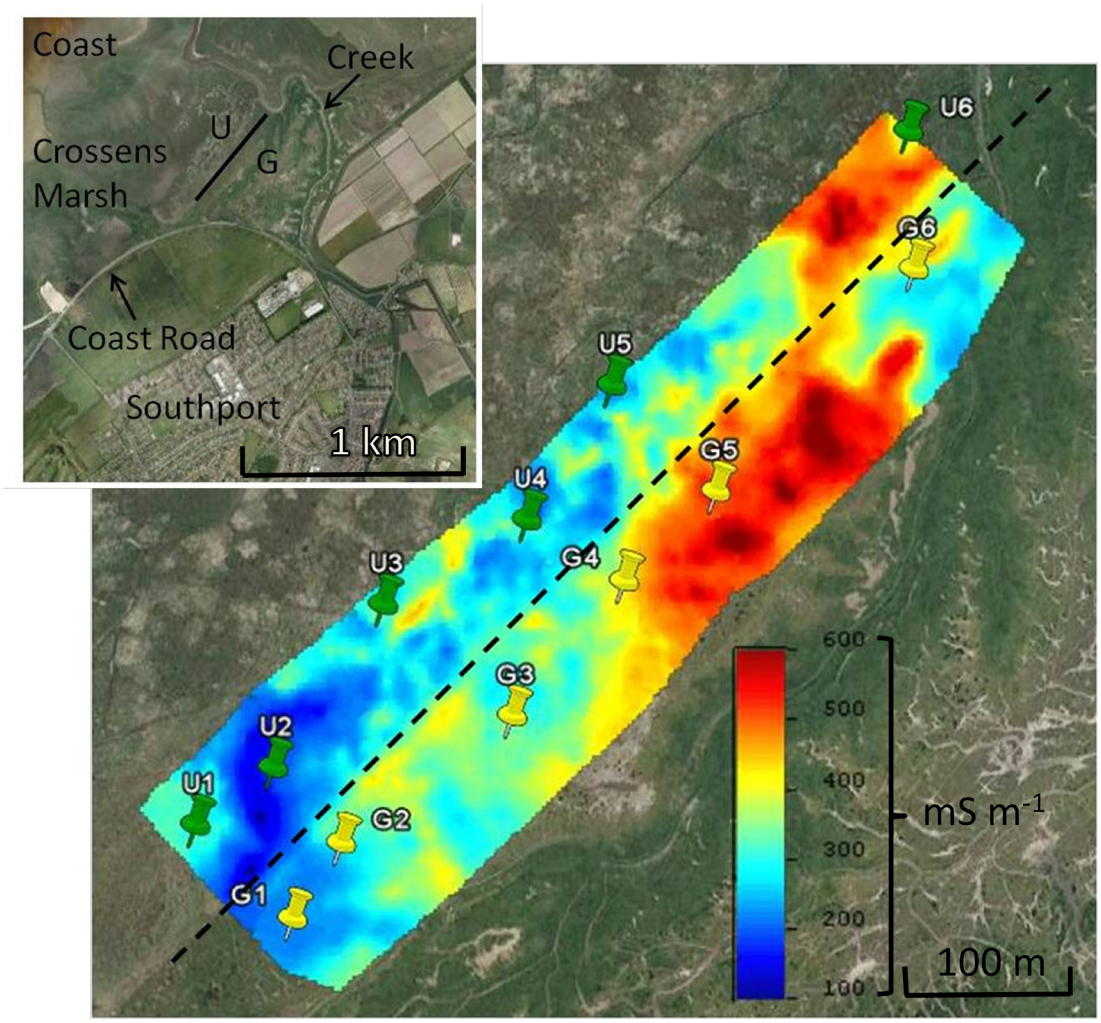

Figure A7.1 Bulk soil electrical conductivity (ECa), a combined measure of soil saturation, salinity and texture for 0-30 cm soil depth, mapped by geophysical electromagnetic induction (EMI) imaging in October 2010 by David Robinson (CEH). Methods as in Moffett *et al*. (2010). This map is a close up of the Crossens marsh field site (inset shows wider area) with the fence line marked by a black dashed line and grazed experimental units (G) by G1-G6 and un-grazed (U) by U1-U6.

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