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Of dwarves and giants

van Klink, Roel

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Of Dwarves and Giants

How large herbivores shape arthropod communities on salt marshes

Roel van Klink

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Chapter 1

General introduction

Roel van Klink

ARTHROPOD CONSERVATION

Arthropods are the most species-rich clade of eukaryotic life forms on earth, with an estimated number of species ranging between 3 and 7 million (Novotny et al. 2002, Hamilton et al. 2010). They play a key role in many ecological processes and have important effects on plant communities (De Deyn et al. 2003, Allan and Crawley 2011). Their central place in all terrestrial food webs makes them an important link between primary producers and vertebrate (top-) predators. Moreover, they perform myriad ecosystem services that human society depends upon, ranging from decomposition and crop pollination to amateur entomology and bird watching (Losey and Vaughan 2006, Prather et al. 2013). Wild invertebrates alone were estimated to account for a yearly economic value of $60 billion in the U.S. alone (Losey and Vaughan 2006), and domesticated bees accounted for another $19 billion (Calderone 2012). Hence, they constitute "the little things that run the world" (Wilson 1987), and ecosystems and human society would soon collapse without arthropods.

Yet, the conservation effort directed towards invertebrates is only a fraction of the effort directed towards the conservation of vertebrates (Wilson 1987, Cardoso et al. 2011), and was thus dubbed "the awkward 'kid sister' to vertebrate conservation" (Dunn 2005). This fails to recognize, however, that due to their vast diversity and often strong specialisation, the majority of species that are endangered or have gone extinct due to human influence must be invertebrates (Dunn 2005). Moreover, it was shown that invertebrates are more prone to be endangered or to go (locally) extinct than either plants or vertebrates (Thomas et al. 2004).

Fortunately, there is an increasing recognition of the conservation value of arthropods. Over the past decades, the effort directed at their conservation has increased considerably, resulting in numerous books (e.g. Samways 1994, 2005, New 2009), high profile publications (e.g. Thomas et al. 2004, 2009, Biesmeijer et al. 2006), and two specialised journals (Journal of Insect conservation and Insect Conservation and Diversity) on this topic.

How the conservation of arthropods should be achieved, though, requires a context specific approach. For each species to persist at a location, its requirements in terms of trophic and non–trophic resources must be met in a spatial and temporal context that can be used by the individuals making op the population (Southwood 1977). The conservation of arthropod species, and any other organism for that matter, should therefore be based on maintaining (or creating) habitats in which required trophic and non-trophic resources are sufficient to retain a viable population (Dennis 2003).

The extreme diversity of arthropods entails an equally large variation in life history traits and, habitat requirements. Contrary to the better known plants and especially vertebrates, these traits and requirements are poorly known for the vast majority of arthropod species, even in the relatively well-studied fauna of Western Europe. To provide conditions meeting the requirements of all species in an ecosystem, and thus to preserve a maximum diversity of arthropods, some form of nature management is often necessary.

GRAZING MANAGEMENT

Most grassland types in Western Europe have a millennia long history of human land use and management (Barker 1985). Interestingly, this long-term extensive land use has led to an extremely high biodiversity (Wilson et al. 2012), and many plant and animal species now depend on the continued existence of these grasslands (Thomas 1993, Thomas et al. 1994). Typically, these grasslands stay in a plagioclimax state (sensu Tansley 1935) due to management actions, and are therefore prone to succession (in most cases to forest) if management is ceased. In most cases, this succession will lead to a decline in plant species richness due to an increasing dominance of tall-statured species (Grime 1973), which is deemed undesirable from a conservation perspective (Bakker 1989). Livestock grazing, as well as mowing or burning, can prevent this succession (Clements 1916), and can maintain plant species richness (Grime 1973). As an increasingly popular management tool to maintain grassland biodiversity, grazing is currently used as management tool in over 500 projects in the Netherlands alone (Alterra 2013). Grazing is often seen as preferable over burning or mowing because large grazers usually display some selectivity in food choice, and can thereby create spatial heterogeneity (McNaughton 1984, Adler et al. 2001). Furthermore, large, charismatic herbivores are seen as a more natural type of grassland management than mowing or burning in Western European landscapes (WallisDeVries 1998), and are seen as replacement for extinct herbivores such as the Tarpan and Aurochs (Bakker et al. 2004, Vera et al. 2006), although this view is heavily debated (Prins 1998, Svenning 2002, Louwe Kooijmans 2012).

The effects of grazing on plant diversity have been synthesised on several occasions (Milchunas et al. 1988, Olff and Ritchie 1998). Generally, in productive systems grazing will increase plant diversity by reducing competitive displacement, whereas in dry, unproductive systems, such as deserts, grazing will decrease plant diversity because of selective grazing for palatable species (Olff and Ritchie 1998, Proulx and Mazumder 1998, Bakker et al. 2006). For arthropods, few attempts at synthesis have been made (but see Morris 2000, Bell et al. 2001), and both positive (Joern 2005, Woodcock and Pywell 2009), negative (e.g. Kruess and Tscharntke 2002a, 2002b) and neutral (e.g. Báldi et al. 2013) effects of grazing on arthropod diversity have been reported in literature. Generally, the importance of structural vegetation complexity is emphasised for both predatory arthropods such as spiders that use aerial plant structures for web building (Gibson et al. 1992b, Bell et al. 2001), and for many herbivorous species that depend on specific plant organs (e.g. Morris 1967, Völkl et al. 1993).

SALT-MARSH CONSERVATION

An interesting grassland ecosystem where grazing management is often deemed appropriate to stem succession to botanically poor, tall vegetation is the coastal salt marsh. Coastal salt marshes are rare and threatened ecosystems that fringe coastlines, estuaries and barrier islands in the temperate zone. Their area has declined worldwide through human influence, in particular by embankments, to which 25-50% was lost in the 20th century alone (Kirwan and Megonigal 2013). The coastal salt marshes of Western Europe are typically productive grasslands subject to tidal and non-tidal flooding by sea water, providing a gradient of increasing inundation frequency with decreasing elevation and a zonation of plant and arthropod communities (Adam 1990, Irmler et al. 2002). These salt marshes harbour a highly specific flora and fauna, confined to this ecosystem due to their adaptations to frequent tidal inundations and high salinity levels (Cheng 1976), and several species endemic to the North Sea basin (R. van Klink & O. Vorst, unpublished data). Salt marshes are therefore of high nature conservation interest, and by harbouring a large proportion of the Western European salt marshes, the Wadden Sea countries have a strong conservation responsibility for this ecosystem.

The zonation of Western European salt marshes typically extends from the most frequently flooded pioneer zone, characterised by *Spartina* and *Salicornia* spp., to the low marsh, dominated by *Puccinellia maritima*, and the only incidentally flooded high marsh, which is typically dominated by salt tolerant glycophytes such as the grasses *Festuca rubra* and *Agrostis stolonifera*, and several halophytic forbs (Beeftink 1977). These salt marshes can be divided into two types: the naturally developed back-barrier marshes, which have a relatively thin clay-layer, and the mostly man-made mainland salt marshes established from sedimentation fields, which have clay layers of several metres thick.

Like many other semi-natural grasslands in Europe, coastal salt marshes have been exploited by humans for several millennia (Bazelmans et al. 2012), primarily in the form of livestock grazing due to the high salinity of the soil. In the second half of the 20th century, however, extensive livestock grazing became less economically feasible, which induced the abandonment of grazing on some marshes, whereas on others intensive livestock grazing continued. The abandonment of grazing led to an increase in the cover of the tall matt forming grasses *Elytrigia atherica* and *F. rubra*, and at lower elevations the dwarf-shrub *Atriplex portulacoides* as well as to a subsequent loss of plant diversity (Bakker et al. 2003). Reinstating grazing management at intermediate densities proved to be an efficient way of restoring plant species richness (Bakker 1985, Bakker et al. 2003) and can create spatial heterogeneity in vegetation structure (Berg et al. 1997).

ARTHROPOD CONSERVATION ON SALT MARSHES

The conservation of arthropods on salt marshes has received only a fraction of the attention that has been directed to plant and bird conservation. Nevertheless, salt-marsh arthropods have enjoyed a long history of scientific study (see Intermezzo).

The effects of grazing on salt-marsh arthropod communities were first investigated at the coast of Lower Saxony, Germany, in a large-scale experiment with cattle grazing at five different densities (0-2 cows ha^{-1}) from 1980-1988 (Irmler and Heydemann 1986, Andresen et al. 1990). This research showed strong negative effects of high stocking densities on most arthropod species, partly due to the inhibited development of the plant community but also strong positive effects of cessation on many arthropod species. However, eight years after cessation of grazing it was shown that the tall grass *Elytrigia atherica* had become dominant, and a number of characteristic salt marsh plants and arthropods had disappeared.

Almost a decade later, this research was followed by a large scale sheep-grazing experiment with five stocking densities (0-10 sheep ha^{-1}) at two locations (Friedrichskoog and Sönke-Nissen Koog) at the coast of Schleswig-Holstein, Germany (Dierßen et al. 1994, Tischler et al. 1994, Meyer et al. 1995, Meyer and Reinke 1996, Kiehl et al. 1996) and with four stocking densities (0-10 sheep ha^{-1}) at the Hamburger Hallig (Stock and Kiehl 2000). It was found that cessation of intensive grazing had a positive impact on plants and arthropods of salt marshes, and led to a salt-marsh management guided by the philosophy "let nature be nature" in salt marshes of Schleswig Holstein (Stock et al. 1997). These experiments are still maintained, although simplified with only three grazing regimes at Friedrichskoog and the Sönke-Nissen-Koog and still four grazing regimes at the Hamburger Hallig. After more than 20 years of stable grazing regimes on the Hamburger Hallig, only at the lowest stocking rate (1 sheep ha^{-1}) the diversity of moths (Microlepidoptera) was not negatively affected by grazing (Rickert 2011, Rickert et al. 2012). Elsewhere in Europe, however, the diversity of beetles and spiders was found not necessarily to be affected negatively by grazing, though large differences in species composition of especially spiders occured (Pétillon et al. 2007, Ford et al. 2013). The dominance of *E. atherica* was shown to increase the occurrence of common inland species, presumably due to an amelioration of the stressful conditions characteristic for salt-marshes (Pétillon et al. 2005, Georges et al. 2011).

SCOPE OF THIS THESIS

The aforementioned research has left many questions unanswered regarding the effects of salt-marsh conservation management on arthropods and their interaction with other organisms. Most importantly, it is currently unknown *which management regime will have the most positive effects on biodiversity*, not only for salt-marsh arthropods, but also for the *plants and birds* depending on this habitat (see also Mandema 2014, Nolte 2014). In particular three questions are of interest: First, the *long-term effects of grazing at intermediate stocking densities* in comparison to high densities and cessation of grazing have so far only been investigated on moth communities (Rickert 2011, Rickert et al. 2012), but not for any other of the salt-marsh inhabiting arthropod groups. Secondly, the choice of *livestock species for grazing management* is an important issue since in the Netherlands horses are increasingly replacing the traditionally used cattle as livestock on salt marshes. Thirdly, it has been suggested that *rotational grazing* with yearly rotations has beneficial effects especially for arthropods (Morris et al. 2005, Farruggia et al. 2012), but this has not been evaluated in productive ecosystems yet.

In order to understand the conservation potential of grazing management, a thorough understanding of the *mechanisms by which large grazers affect arthropod communities* is required. The aim of this thesis is, therefore, to answer these gaps in knowledge with a strong focus on mechanistic aspects, ultimately leading to evidence-based management recommendations.

The mechanisms by which arthropods are affected by grazing management are mostly, but not exclusively, mediated by changes in the plant community such as changes of vegetation structure and plant species richness (Fig. 1.1). Changes in arthropod communities caused by large herbivores can be expected to also affect higher trophic levels, most notably insectivorous birds. These also depend on the physical structure of the vegetation, which is modulated by herbivores. This thesis should therefore be seen in close association with the work of Nolte (2014) on the vegetation and Mandema (2014) on birds (Fig. 1.1), which were largely performed at the same field sites. In 2010, a large-scale, triplicate grazing experiment was installed at the Dutch Wadden Sea coast to compare the effects of grazing by horses and cattle at low (0.5 animal ha-1) and high densities (1 animal ha-1), on plant, arthropod and bird diversity simultaneously (for details see chapter 6).

Ultimately, the knowledge gained will be applicable to optimize the management of salt marshes for the conservation of arthropod diversity, but also diversity of plants and birds, and ideally also other grazed ecosystems.

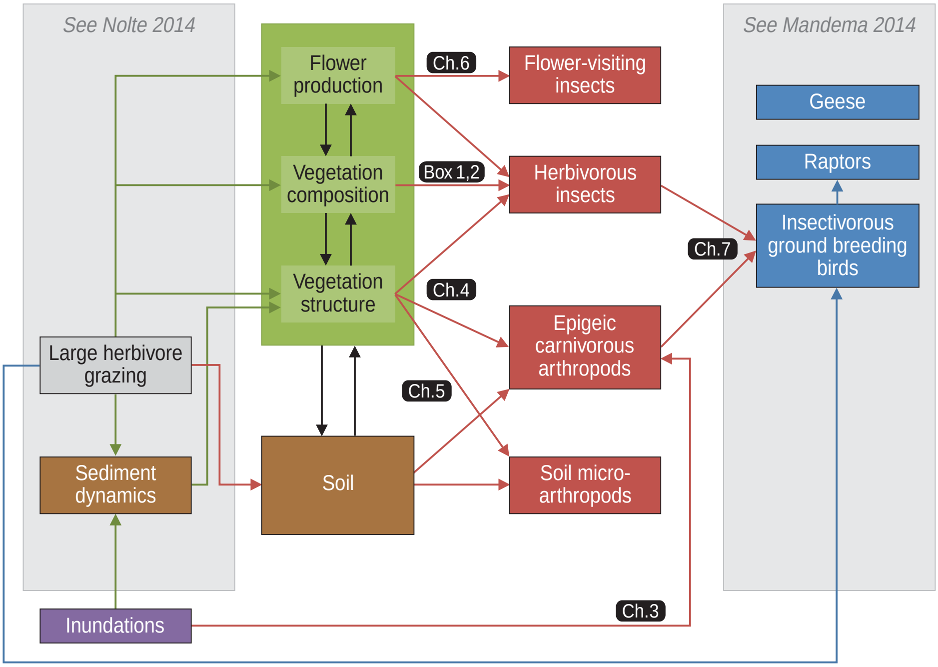


Figure 1.1 A schematic representation of the contents of this thesis and its relation with the studies of Nolte (2014) and Mandema (2014), performed at the same experimental field site. Chapter 2 is a review of published literature.

THESIS OUTLINE

In **chapter 2** an overviewof the broad, but poorly integrated field of arthropods in grazed grasslands by reviewing literature from a wide range of ecosystems published until 2013 is presented. Apart from providing a quantitative analysis of the effects of large grazers on arthropod diversity in comparison with plant diversity, we also set this knowledge in a mechanistic framework, which allows us to identify gaps in knowledge and to design a research agenda.

Chapter 3 deals with the interaction between abiotic stress and the presence or absence of large grazers and their effects on ground beetles, spiders and shore bugs. This research was done on the mainland marsh of Noord-Friesland Buitendijks, where a varied grazing management existed, and on the well-studied island marsh of Schiermonnikoog (Fig. 1.2) where both grazed and ungrazed salt marshes are present.

The unresolved question of effects of heterogeneity induced by large grazer (patches of tall and short vegetation) on plant and arthropod communities is answered in **chapter 4**. Here, differences in the effects of heterogeneity to the effects of intensively grazed homogeneous short vegetation and ungrazed homogeneous tall vegetation were studied at three sites at the northern German Wadden Sea coast (Fig. 1.2).

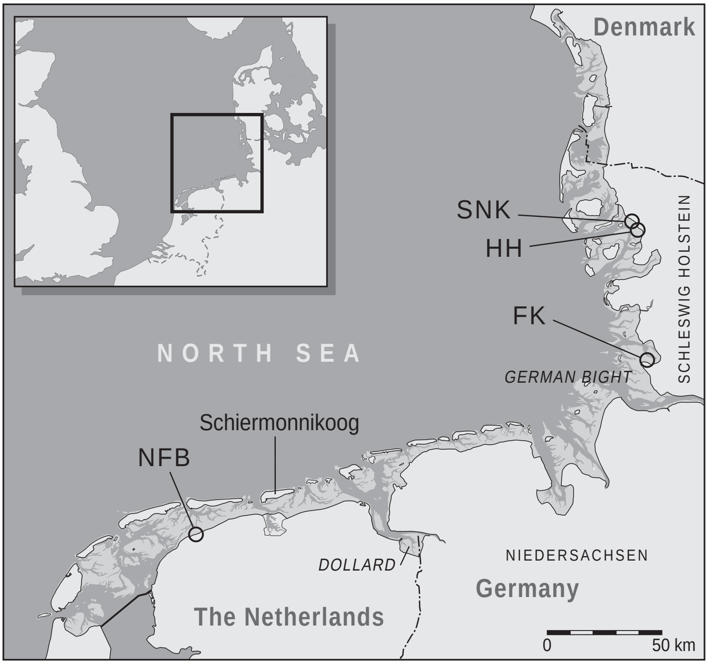


Figure 1.2 Locations of the study sites visited for this thesis. NFB: Noord Friesland Buitendijks; FK: Friedrichskoog; HH: Hamburger Hallig; SNK: Sönke-Nissen Koog.

Chapter 5 focuses on the effects of soil compaction and defoliation on soil fauna and epigeic fauna in conjunction with abiotic conditions and plants in a manipulative study.

Chapter 6 returns to the application of grazing management for arthropod conservation and compares the effects of management using cattle and horses at different stocking densities on flower-visiting insects. Moreover, preliminary effects of rotational grazing management are presented. These studies were done at a grazing experiment at Noord Friesland Buitendijks at the Dutch Wadden Sea coast, which was established in 2010 (Fig. 1.2).

In a field setting (**box I**) and a manipulative study (**box II**) the determinants of richness and abundance of herbivorous insects of five halophytes were investigated.

Chapter 7 gives a multitrophic perspective of the effects of vegetation structure on arthropods as a resource for breeding birds on the grazed salt marshes of Noord Friesland Buitendijks (Fig. 1.2).

In **chapter 8** I will synthesise the knowledge gained and provide a mechanistic understanding of the effects of large grazers on arthropod communities and species (**box III**). This results in specific recommendations for the management of salt marshes, which will also be put in perspective of the management requirements of plants and birds.

This study has generated a vast amount of meta-data regarding the occurrence of many arthropod species at the investigated sites. These datasets have been complemented with a large number of hand catches performed by myself and several taxonomic specialists. The result is an extensive list of the arthropod species occurring at Noord-Friesland Buitendijks. This preliminary list can be found in the **Appendix** and is in preparation for publication.

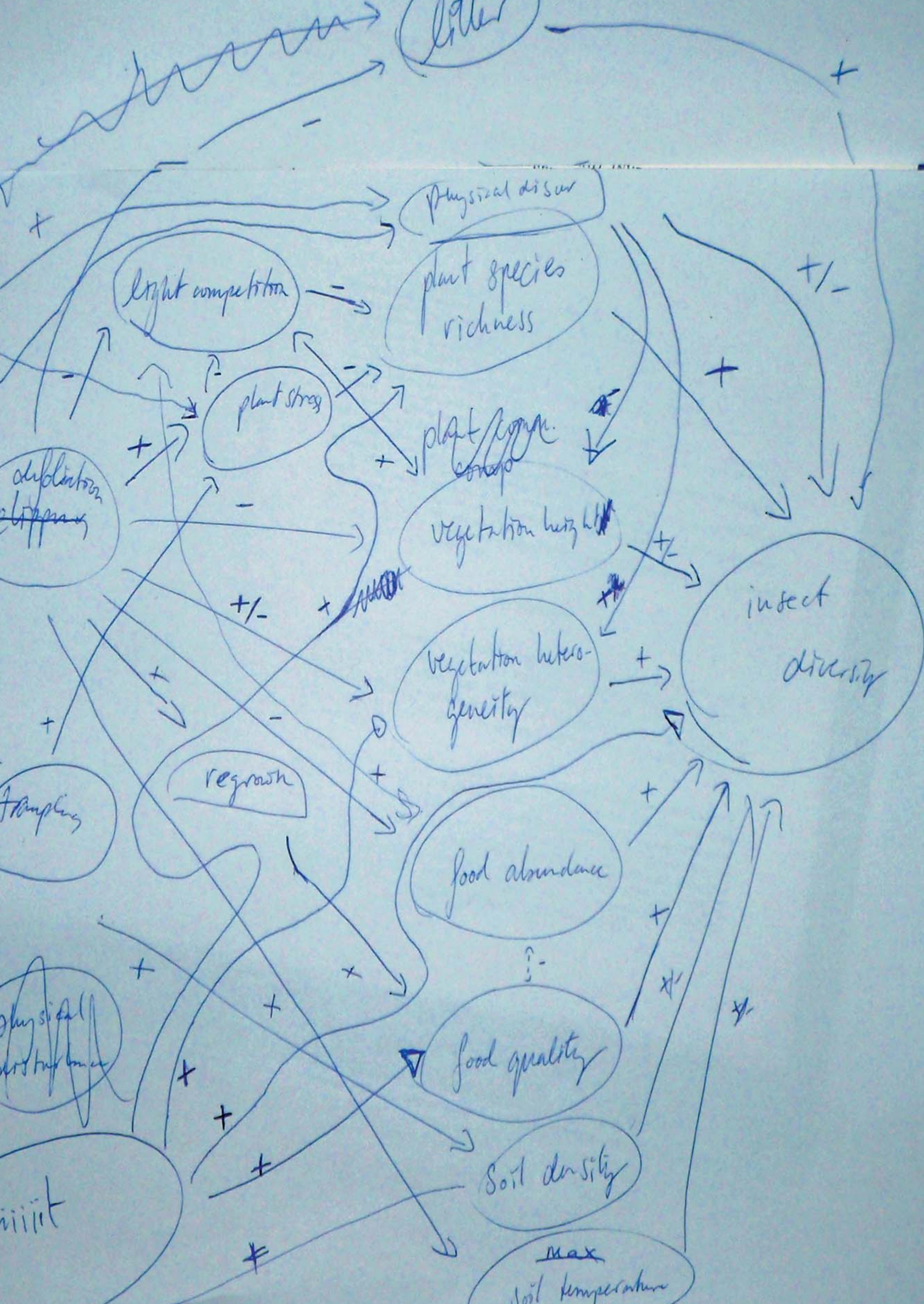
INTERMEZZO: A short history of research on salt-marsh arthropods

In the 1960s and 1970s there was a strong interest in the life-history adaptations of terrestrial arthropod species to the adverse conditions present on salt marshes (e.g. Bethge 1973, Regge 1973, Foster and Treherne 1976, Treherne and Foster 1977, Heydemann 1979), ultimately culminating in a book on the subject (Cheng ed. 1976). Moreover, two-and-a-half centuries of taxonomic and faunistic research yielded a wealth of knowledge on the habitat affiliations of European invertebrate species, providing a good knowledge base for ecological research.

In those days, also the changes in arthropod communities following the embankment of salt marshes for reasons of land-reclamation or coastal protection received attention (Heydemann 1960, 1962, Meijer 1973, Verschoor and Krebs 1995a, 1995b). Fortunately, these large-scale embankment projects were abandoned after the 1980s, since the conservation value of salt marshes as unique and important nature reserves was increasingly acknowledged.

Salt-marsh arthropods have also been subjects of the study of many different fundamental ecological processes, such as dispersal (e.g. Raupp and Denno 1979, Denno et al. 1996, Bonte et al. 2007), community structure (e.g. Stiling and Strong 1983, Irmler et al. 2002, Moon and Stiling 2002a, Finke and Denno 2004), primary succession (Schrama et al. 2012) and population genetics (e.g. Desender et al. 1998, Dhuyvetter et al. 2007). This interest in such a rare ecosystem is probably due to its unique characteristics of being poor in species, simple in architecture and disjunct in its distribution, separated by hostile habitat of land and sea, and because of its characteristic stress gradient.

The most recent literature also reports on the invertebrates affected by the 2011 BP oil spill in the gulf of Mexico (McCall and Pennings 2012). This work showed strong negative effects of the oil spill, but also a remarkable recuperative ability of the affected invertebrate fauna.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Chapter 2

Effects of large herbivores on grassland arthropod diversity

Roel van Klink, Fons van der Plas*, Toos van Noordwijk*,
Michiel F. WallisDeVries, Han Olff

*These authors contributed equally to this work

ABSTRACT

Both arthropods and large grazing herbivores are important components and drivers of biodiversity in grassland ecosystems, but a synthesis of how arthropod diversity is affected by large herbivores has been largely missing. To fill this gap, we conducted a literature search, which yielded 141 studies on this topic of which 24 simultaneously investigated plant and arthropod diversity. Using the data from these 24 studies, we compared the responses of plant and arthropod diversity to an increase in grazing intensity. This quantitative assessment showed no overall significant effect of increasing grazing intensity on plant diversity, while arthropod diversity was generally negatively affected. To understand these negative effects, we explored the mechanisms by which large herbivores affect arthropod communities: direct effects, changes in vegetation structure, changes in plant community composition, changes in soil conditions, and cascading effects within the arthropod interaction web.

We identify three main factors determining the effects of large herbivores on arthropod diversity: 1) unintentional predation and increased disturbance, 2) decreases in total resource abundance for arthropods (biomass) and 3) changes in plant diversity, vegetation structure and abiotic conditions. In general, heterogeneity in vegetation structure and abiotic conditions increases at intermediate grazing intensity, but declines at both low and high grazing intensity.

We conclude that large herbivores can only increase arthropod diversity if they cause an increase in (a)biotic heterogeneity, and then only if this increase is large enough to compensate for the loss of total resource abundance and the increased mortality rate. This is expected to occur only at low herbivore densities or with spatio-temporal variation in herbivore densities.

As we demonstrate that arthropod diversity is often more negatively affected by grazing than plant diversity, we strongly recommend considering the specific requirements of arthropods when applying grazing management and to include arthropods in monitoring schemes. Conservation strategies aiming at maximising heterogeneity, including regulation of herbivore densities (through human interventions or top-down control), maintenance of different types of management in close proximity and rotational grazing regimes, are the most promising options to conserve arthropod diversity.

Biological Reviews in press

INTRODUCTION

Large grazing herbivores exert major influences on their habitat and are abundant and important in all grassland ecosystems (Hobbs 1996, Olff et al. 2002). Populations and communities of large herbivores have been under human influence for millennia, with humans causing extinctions (Owensmith 1989, Lorenzen et al. 2011, Rule et al. 2012) and changes in abundances (Owensmith 1989). Additionally, ever since the first goats and sheep were domesticated over 11000 years ago (Zeder 2008) agricultural livestock practices have intensified, culminating in the year 2000 in 26 % of the terrestrial biome being used for livestock production as pasture or fodder crops (FAO 2008). This may pose a threat to biodiversity through overgrazing (e.g. Smith 1940), and habitat loss and fragmentation (e.g. Kruess and Tscharntke 1994, Fahrig 2003). Conversely, in many semi-natural types of grassland, especially in Europe, the maintenance or reintroduction of large herbivores is a widely applied management tool, aiming to preserve an open, species-rich landscape (WallisDeVries 1998, Ostermann 1998). In these systems, livestock is thought to replace ecological functions of now-extinct native herbivores such as aurochs and tarpan (Bakker et al. 2004). Grazing thus has a large impact on a global scale and in many areas grazing regimes have recently changed due to agricultural intensification (increased stocking rates), agricultural abandonment (EEA 2004) and changes in wild herbivore assemblages (Campbell and Borner 1995, Donlan et al. 2006). It is therefore imperative to understand the influence of large grazing herbivores on the biodiversity of various plant and animal groups.

Effects of grazing on plant diversity are variable, with literature supporting both positive and negative effects (Milchunas, Sala & Lauenroth, 1988; Olff & Ritchie, 1998). Reported effects on arthropod diversity are equally diverse, with studies reporting negative (e.g. Kruess & Tscharntke, 2002a,b; Pöyry et al., 2004), positive (Joern 2005, Woodcock and Pywell 2009), or neutral (Bestelmeyer and Wiens 2001, Hofmann and Mason 2006) effects of large herbivores. Intuitively, a strong positive relationship between the diversity of resources (plants) and consumers (arthropods) would be expected (Murdoch et al. 1972, Tilman 1986), but evidence is mounting that the response of arthropod diversity to grazing deviates from that of plant diversity (e.g. Kruess and Tscharntke 2002a, Pöyry et al. 2006, Zhu et al. 2012). For plants, a number of mechanisms underlying the effects of grazing on diversity have been identified, and general frameworks bringing these mechanisms together have been proposed (Milchunas et al. 1988, Olff and Ritchie 1998). Such a framework is largely missing for understanding effects of large herbivores on arthropod diversity (but see e.g. Morris 2000, Bell et al. 2001), despite the fact that arthropods constitute the most species-rich eukaryotic group on earth, are responsible for myriad ecosystem services (Prather et al.,2013) and take a central place in all terrestrial food webs (Seastedt and Crossley 1984).

In this review we explore the patterns and processes of grassland arthropod responses to large herbivores. First, we present an overview of published literature in terms of taxonomic, geographic and experimental focus in published research, and perform a quantitative review in which we compare the responses of arthropod and plant diversity to grazing. Next, we classify the mechanisms through which large herbivores affect arthropod diversity. The resulting framework includes both direct effects (such as disturbance and incidental predation) and indirect effects (through modifications of soil and vegetation properties) of large herbivores on arthropod communities. Finally, we synthesise these effects, discuss the implications for conservation of arthropod diversity and identify remaining questions.

We focus this review on the effects of large herbivores on *aboveground* arthropod communities in *open landscapes* and on *ecological* time scales. Obviously, large herbivores also affect belowground communities (as reviewed by Bardgett & Wardle 2003), play a role in forested landscapes (included in the review by Suominen & Danell 2006) and have co-evolutionary relations with grassland plants (McNaughton 1984, Milchunas et al. 1988) and arthropods (e.g. Siegfried 1990). Given these earlier syntheses, these habitats, ecosystem compartments and evolutionary time scales fall outside the scope of this review. Other potentially important drivers of the diversity of grassland arthropods, such as burning and hay-making have been included in reviews by Morris (2000), Littlewood, Stewart & Woodcock (2013) and Joern & Laws (2013), and are, therefore, not considered here either. Large-scale patterns and processes, such as landscape characteristics and meta-community dynamics have recently been reviewed and synthesised by Tscharntke et al. (2012).

QUANTITATIVE RESPONSE OF ARTHROPOD DIVERSITY TO GRAZING

In order to get an overview of taxonomic spread, geographic location, and experimental design in studies reporting on the impact of large herbivores on arthropod diversity, we searched published literature for publications on this topic. Of the publications found, we used a sub selection (those that simultaneously assessed response of arthropod and plant diversity to grazing) to quantitatively assess 1) whether the response of arthropod diversity to grazing differs from that of plant diversity, and 2) whether the response of arthropod diversity is related to the response of the plant community, ecosystem productivity or differences in experimental design among studies.

Literature search

We performed a systematic search (Pullin and Stewart 2006) for papers on effects of grazing by large herbivores on arthropod species richness, comparing different grazing intensities, species or breeds, or which compared grazing to other forms of conservation management such as burning, haying or abandonment. Only studies meeting the following three criteria were assessed: 1) published or in press in international, peer-reviewed scientific journals in Thomson Reuters Web of Science, accessible to the University of Groningen; 2) performed in (semi)-natural grass- or heathland ecosystems; 3) with arthropods identified to species level. Studies in which grazing effects were potentially confounded with other variables (such as soil composition or climate) were omitted. We initially used cross-referencing to get an overview of the groups of arthropods commonly assessed, and finally performed searches on each of these groups, as well using general search terms "insects", "arthropods" and "invertebrates" (see Table S1 in the online supporting information accompanying the article) in combination with "graz*" in Thomson Reuters Web of Science.

Dataset description

Our search yielded 141 studies assessing the effects of large herbivores on arthropod communities published between 1940 and May 2013, sometimes in combination with other management types (Table S1). An overview of the taxonomic and geographic focus of all 141 studies is given in Fig. 2.1. Ground beetles, butterflies and grasshoppers have been studied most extensively, while other, sometimes extremely species-rich groups, such as parasitic Hymenoptera, (non-syrphid) flies and aphids have received virtually no attention (Fig. 2.1A). More than half of the studies assessed only one taxonomic group, with less than 25% of studies assessing more than two arthropod taxa (Fig. 2.1B). The number of years that arthropods were sampled during these studies varied: in about half of the studies arthropods were sampled for only one year while only during two studies were data collected for eight years or more (Fig. 2.1C).

The majority of grazing studies were conducted in Europe (>65%; Fig. 2.1D), where domestic grazer populations are often managed for nature conservation purposes. In North America (21%) and Africa (5%) grazing studies are also regularly conducted, often focusing on the effects of wild herbivores, sometimes in comparison to domestic livestock. Studies from Oceania, Asia and South America are rare, although several studies from these continents have been published on grazing effects in wood- or scrublands (Table S2). More than half of the studies were published after the year 2002 (Fig. 2.1E).

Studies of the effects of large herbivores on arthropod diversity could roughly be divided into two types: controlled experimental approaches and historic studies. In controlled experiments, a comparison was made between experimental plots receiving (randomly assigned) treatments differing in stocking density or grazing species (e.g. Gibson et al., 1992; Dennis et al., 1997; Joern, 2005; Rickert et al., 2012). These include studies using exclosures to exclude some or all vertebrate herbivores within sites (e.g. Morris, 1967; Fisher Barham & Stewart, 2005; Gómez & González-Megías, 2007). The controlled experiments usually ran for less than ten years (although some impressive examples of long-term experimental grazing research exist, see Table S1) and generally had a relatively small number of replicates (maximum three). In the historical studies, effects of grazing were compared among a number of sites that differed historically in densities or species of herbivore (e.g. Smith, 1940; Kruess & Tscharntke, 2002a, b; Nickel & Hildebrandt, 2003). Here, the number of replicate sites and the geographical extent were usually larger, but the sites did not necessarily have a constant grazing pressure or identical starting conditions. In our database, experimental and historical studies were represented approximately equally.

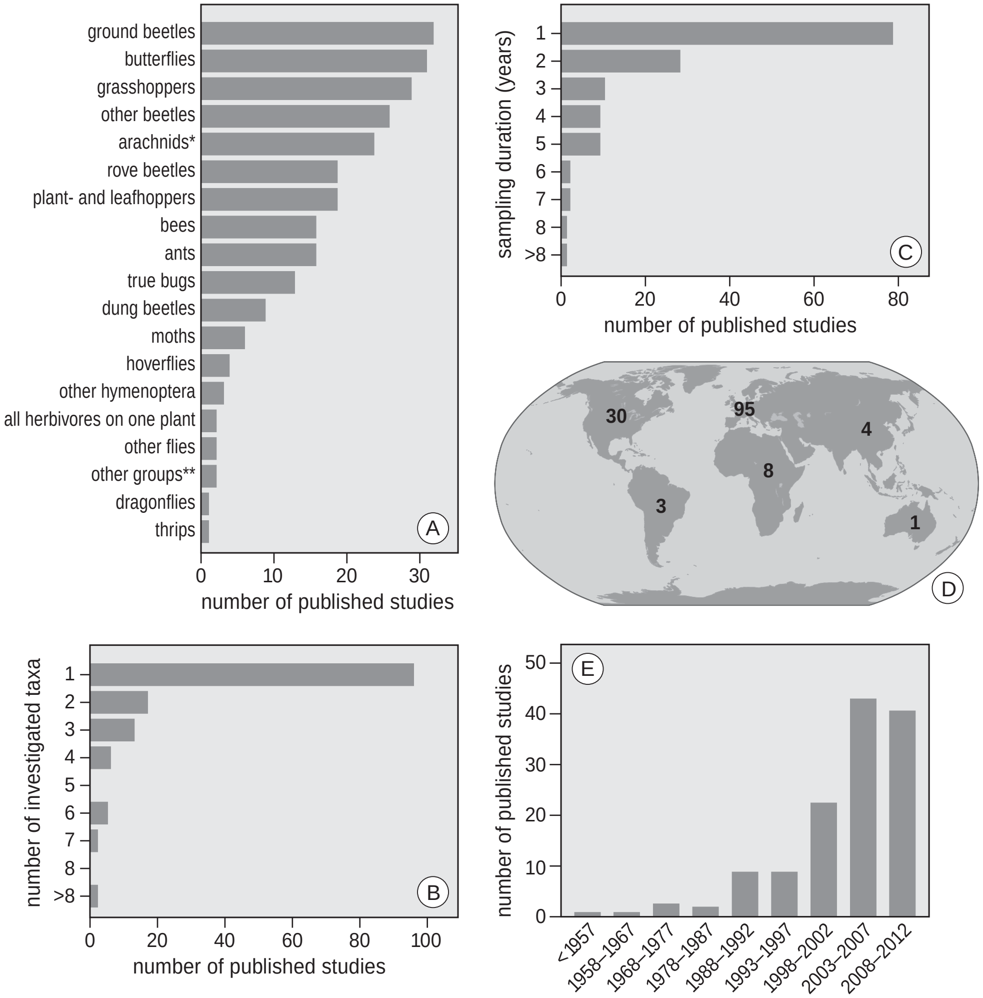

Figure 2.1 Research focus of 141 published studies assessing effects of large herbivores on arthropod diversity, conducted in open landscapes (grass- or heathlands), with arthropods identified to species level: A) studied taxa, B) taxonomic spread (number of investigated taxa), C) duration of sampling, D) geographic location, and E) year of publication (until 2012). We documented the identity of the most commonly assessed taxonomic groups (usually to order level, but sometimes to family or class level, see Table S3 in the online supporting information. A complete list of the analysed studies and definitions of arthropod groups can be found in Table S1 and S3 respectively. *Arachnids: spiders, harvestmen, pseudoscorpions; **Other groups: Mantodea, Phasmatodea, Neuroptera, Dermaptera etc.

Statistical analysis

For the quantitative assessment of grazing effects on arthropod diversity we used all studies that reported the response of both arthropod and plant diversity to different grazing intensities, including no grazing (24 of the initial 141 studies). This selection included 21 studies conducted in Europe, one in Africa, and two in the Americas. Ecosystems ranged from prairies and savannahs to coastal salt marshes and alpine grasslands, all of which had a history of grazing of at least several decades. Both experimental and descriptive approaches were represented. From these studies we extracted the reported numbers of plant and arthropod species found under each grazing treatment. In three cases effects on plant diversity were extracted from other publications about the same experiment, and in four cases effects on plant diversity were obtained directly from the authors. For studies where plant or arthropod richness responses to grazing were only reported in graphs, we used the ImageJ software (Abramoff et al. 2004) to extract accurate estimates of richness.

We performed two separate linear mixed model analyses to analyse the relation between plant and arthropod diversity in response to grazing. As the response variable, we used untransformed response ratios of the change in richness with an increase in grazing intensity ($\frac{r_2 - r_1}{r_1}$, where r_1 = richness at lower grazing intensity and r_2 = richness at higher grazing intensity), because these better approximated a normal distribution than log-transformed response ratios (Hedges, Gurevitch, & Curtis, 1999; see also Milchunas & Lauenroth, 1993; Wardle et al., 2001). When responses of multiple arthropod taxa were reported (10 studies), we used the response ratio averaged over all taxa so that changes in comparatively species-poor taxa (e.g. butterflies) would not be overshadowed by changes in species-rich taxa (e.g. beetles). Therefore, only one data point per comparison between two grazing levels was included per study. When more than two grazing intensities were reported in a study, all pairwise comparisons were included as separate data points, as were multiple sites per study (whenever reported separately). This resulted in a total of 61 data points. A complete list of the analysed studies and definitions of arthropod groups can be found in Table S1.

First, we tested whether plant and arthropod diversity responded differently to grazing management, using taxonomic group (arthropod/plant) as a fixed factor and “data point” nested in “publication” as a random factor. Secondly, we analysed which variables explained the response of arthropod diversity to an increase in grazing intensity. For this analysis we used the same response variable for arthropods described above and “publication” was again used as random factor. As explanatory variables we included response ratio of plant diversity and productivity of the study system, and as covariates we included the type of experimental design (duration of the grazing treatment, nature of the study (experimental or descriptive), and the difference in grazing intensity studied). These variables were included as they are known to affect the response of plant diversity to grazing (Milchunas et al. 1988, Olff and Ritchie 1998, Proulx and Mazumder 1998, Bakker et al. 2006). Duration of treatment was included as the number of years since the most recent management change. Productivity and difference in grazing intensity between compared treatments were included as ordinal variables and estimated from the site descriptions (productivity: ‘1’ for unproductive systems such as steppes and heathlands, ‘2’ for mesotrophic grasslands and ‘3’ for productive systems such as savannahs, floodplains and salt marshes; difference in grazing intensity: ‘1’ indicates a small difference in herbivore density, for instance low versus moderate density, whereas ‘3’ indicates a large difference in density e.g. ungrazed versus intensively grazed, ‘2’ was used for intermediate differences). Interaction terms were not included, as there was no a priori, biological reason to assume any of these to be of particular relevance. To obtain an estimate of the variation explained by this second model, we obtained a pseudo-r^2 using the recently published method for mixed models (Nakagawa and Schielzeth 2013) using the MuMIn package for R (Barton 2013). This gives the "marginal r^2", which represents the variance explained by the fixed factors, and the "conditional r^2", representing the variance of both the random and the fixed factors. All analyses were performed in R 2.14.1 (R Core Team, 2013), with use of the lme4 package (Bates et al. 2013).

Results

There was large variation in response of both plant and arthropod diversity to grazing (Fig. 2.2A). Across all studies, arthropod diversity responded significantly negatively to an increase in grazing intensity (GLMM: $\mu = -0.14 \pm 0.04$, $t = -3.36$, $p = 0.002$, Fig. 2.2A), with over 80% of the data points showing a decrease in richness. Plant diversity, however, did not show a significant response to grazing (GLMM: $\mu = 0.04 \pm 0.04$, $t = 0.98$, $p = 0.33$), with approximately as many positive responses as negative ones (Fig. 2.2B). When the two effects were compared, the response of arthropod diversity was significantly more negative than that of plant diversity (GLMM: $\mu = -0.15 \pm 0.03$, $t = 4.54$, $p < 0.001$, Fig. 2.2A). The second mixed model, including multiple explanatory variables, revealed a significant, but

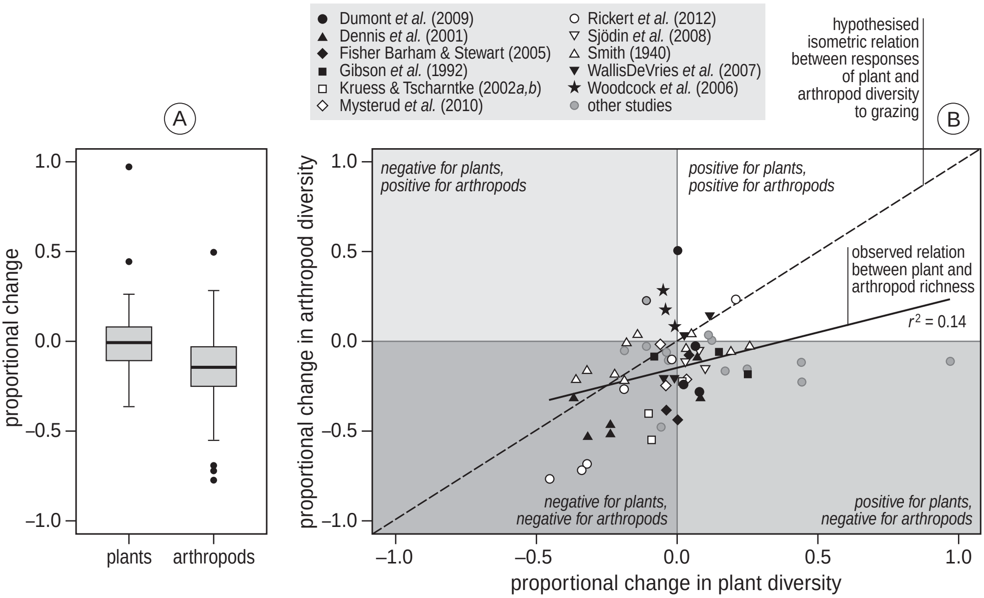

Figure 2.2 Comparison of the response ratios of plant and arthropod diversity to an increase in grazing intensity (median ± interquartile range, whiskers represent 1.5*interquartile range, dots represent outliers) (A) and the relationship between these response ratios (B). Data were extracted from 24 studies published between 1940 and 2013 reporting on the effects of grazing on both plant and arthropod diversity, supplemented with data obtained from several authors (see Table S1).

weak positive relationship between the responses of plant and arthropod diversity to grazing (β = 0.41 ±0.13, t = 3.28, p = 0.004, model fit: χ^2 = 9.65, p = 0.002 Fig. 2.2B), with a negative intercept (μ = -0.15 ±0.04). We found no significant effect of ecosystem productivity (χ^2 = 1.21, p = 0.55), study duration (χ^2 = 6.98, p = 0.14), experimental type (χ^2 = 0.56, p = 0.45), or difference in grazing intensity (χ^2 = 3.94, p = 0.27). The variation explained by the model was relatively low. The fixed variables (marginal r^2) explained only 14% of the variation, but the fixed and random variables combined (conditional r^2) explained 55% of the total variation, indicating large variation in response to grazing between studies.

MECHANISMS UNDERLYING GRAZING EFFECTS ON ARTHROPOD DIVERSITY

The quantitative analysis in the previous section showed that 1) the prevailing effect of large herbivore grazing on arthropod diversity is negative, 2) within studies, arthropod diversity responds more negatively to grazing than does plant diversity, 3) the response of plant diversity to grazing is a poor predictor for the response of arthropod diversity and 4) there is large variation in the effects of grazing on arthropod diversity. None of the covariates included in our model (productivity of the study system, duration of the grazing treatment, nature of the study (experimental or descriptive) and the difference in grazing intensity studied) proved significant. This may indicate that these factors are not of major importance in determining arthropod richness changes in response to grazing. However, because of the size of the dataset and the frequently limited accuracy of estimates (especially for productivity) caution is advised when drawing conclusions and more research may be required. The majority of variation explained by our mixed model was due to the differences between studies (random effects). Differences between focal arthropod groups might be one of the main sources of this random variation. Arthropods form a large, heterogeneous group with a broad diversity in life history traits and different groups have repeatedly been shown to differ in their sensitivity to changes in habitat characteristics (Oertli et al. 2005, Dauber et al. 2005).

In order to understand these patterns, we will focus on the potential mechanisms by which large herbivores affect arthropod species. Fig. 2.3 shows a conceptual framework of direct and indirect pathways through which herbivores can affect arthropods. The impact of these pathways on arthropod diversity is mediated by the three ecological determinants of the populations that constitute a community: (1) abiotic conditions of the environment (including non-trophic use of biotic structures), (2) trophic resource availability and (3) predation (Chase and Leibold 2003). We use these determinants to classify the mechanisms by which arthropods are affected.

Direct effects

Large herbivores can affect arthropod diversity directly through unintentional ingestion or trampling (Fig. 2.3, path1), but also by supplying resources for specialised groups such as

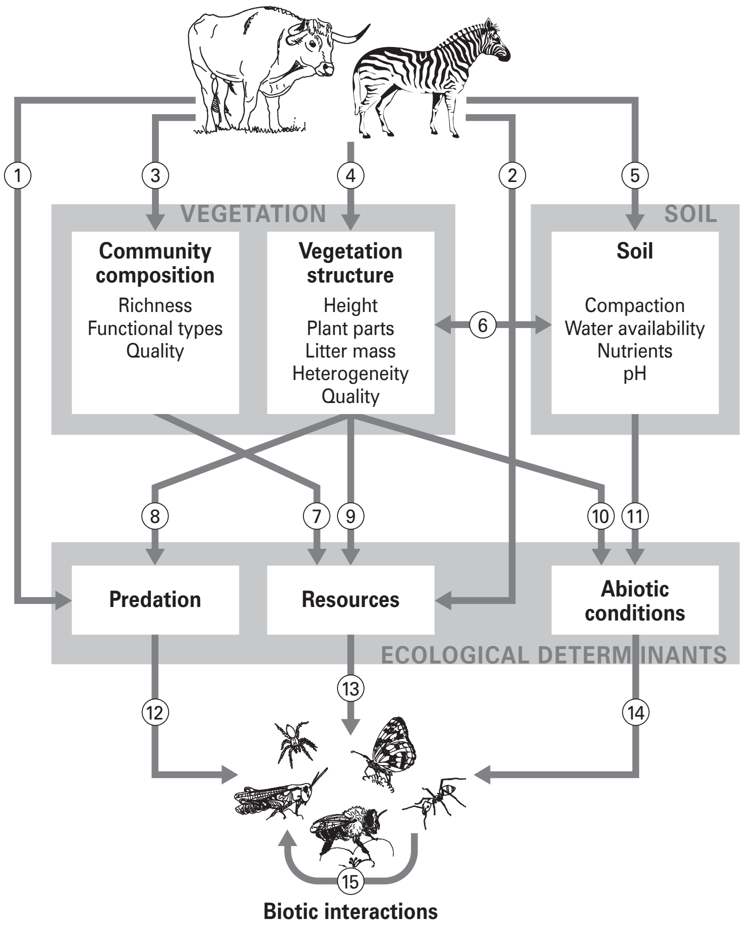

Figure 2.3 A conceptual framework of the mechanistic pathways by which large herbivores directly and indirectly affect arthropod diversity. Arrows represent mechanisms. The first row of boxes represents biotic and abiotic conditions that are modified by large herbivores; the second row of boxes represents the mechanisms operating on arthropod individuals, populations and communities. 1, direct effects: trampling and unintentional predation (Section III.1); 2, direct effects: dung, carcasses, blood, live tissue (Section III.1); 3, increase or decrease in plant species richness and changes in functional groups, the direction of which depends on large herbivore density and ecosystem properties (Section III.3); 4, changes in vegetation structure: lowering of vegetation height through defoliation and changes in horizontal heterogeneity resulting from herbivore selectivity (Section III.2); 5, changes in soil conditions (pH, bulk density) (Section III.4); 6, changes in soil conditions can affect vegetation characteristics (Section III.4); 7, changes in plant species richness can affect species richness of associated insect herbivores (Section III.3); 8, a reduction in vegetation height can increase predation risk by vertebrate predators (Section III.2); 9, direct competition for resources between the base of the arthropod food web and large herbivores (Section III.2); 10, a reduction in vegetation height increases surface temperatures, but decreases shelter from climatic extremes and essential structures for egg deposition or web construction (Section III.2); 11, changing soil properties may affect insects that spend part of their lives below ground (Section III.4); 12,13,14, the combined changes in abiotic conditions, resources and predation determine the effects on each arthropod species, thereby affecting species richness; 15, due to the interactions between arthropod species, changes in species' abundances may have cascading effects on other species, with ultimate effects on total arthropod species richness.

dung feeders and scavengers (Fig. 2.3, path 2). Each of these mechanisms will be discussed here briefly.

Large herbivores frequently ingest arthropods as a byproduct of their forage intake. Such unintentional predation can lead to reduced arthropod population sizes (Gómez & González-Megías, 2007; Bonal & Munoz, 2007; Van Noordwijk et al., 2012b)The potential consequences at the community level have rarely been measured, but defoliation by mowing is known to cause high direct arthropod mortality (reviewed by Humbert et al. 2009). Gómez and González-Megías (2007) demonstrated large differences between guilds of herbivorous insects in susceptibility to unintentional predation. While endophagous insects (living within plant structures) often were ingested by large herbivores, ectophagous insects (living on plants) were generally not affected. Aphids and ladybirds, for example have been shown to avoid ingestion by dropping off the plant when detecting the breath of large vertebrates (Gish et al. 2010, Ben-Ari and Inbar 2013). However, in short vegetation with limited possibilities to escape and during immobile life-stages (eggs and larvae) also ectophagous species may be ingested (Van Noordwijk et al. 2012). These differences in the vulnerability to incidental ingestion among arthropod guilds suggest a large potential for shifts in arthropod communities.

Large herbivores also cause direct disturbance while moving through their habitats, which is most evident in the form of trampling living vegetation, litter and soil (Cumming & Cumming, 2003; Hobbs, 2006, Fig. 2.3, path 1). Knowledge on the extent to which this affects arthropods is limited, but there is some observational (Chappell et al., 1971; Bayfield, 1979; Bonte & Maes, 2008; Woodcock & Pywell, 2009) and experimental (Duffey 1975) evidence that trampling by herbivores or humans mostly negatively affects population sizes and diversity of arthropods. It is not always clear, however, whether these effects resulted directly from direct trampling on arthropods, or indirectly, through changes in soil, litter or plant characteristics (see also section 3.2 and 3.3). Duffey (1975) demonstrated convincingly that even low frequencies of 5-10 treads per month on litterbags were highly detrimental to the arthropod fauna, and Chappell et al. (1971) showed large decreases in faunal abundance between lightly and heavily trampled calcareous grasslands. For less mobile arthropods, such as caterpillars, but also for large dung beetles (Negro et al. 2011) trampling could be an underestimated direct source of mortality (Fig. 2.2, path 1). Additionally, frequent disturbance by large herbivores may decrease habitat suitability for arthropods. This may again be of greater importance for less mobile species that could experience difficulties in returning to their host plants, like many larval insects (Dennis, Young & Gordon, 1998; Kruess & Tscharntke, 2002a), and may even be evident at low herbivore density, when no measurable effect on vegetation characteristics is documented (Kruess and Tscharntke 2002b).

Conversely, large herbivores may have positive effects by directly supplying resources to arthropods in the form of dung, carcasses, blood and living tissue (Fig. 2.2, path 2). Studies investigating the effect of dung on arthropod communities mostly focused on dung beetles, despite the fact that also termites (Freymann et al. 2008) and various fly families also feed on dung. Not surprisingly, these studies often report positive effects of large-herbivore presence on dung beetle diversity and abundance (Lumaret et al. 1992, Verdu et al. 2007, Jay-Robert et al. 2008), but too high herbivore densities may be detrimental to dung beetle abundance and diversity (Jankielsohn et al. 2001, Negro et al. 2011). Differences in dung beetle diversity between livestock grazing and natural herbivore assemblages have been reported to be small, although community composition can differ between areas with different herbivore assemblages (Jankielsohn et al. 2001, Numa et al. 2012). Effects of livestock management on dung feeding fauna is also strongly influenced by the use of antiparasitic medication, which has highly detrimental effects on dung feeding fauna (Wall and Strong 1987, Madsen et al. 1990) and dung decomposition rates (Wall and Strong 1987, Beynon et al. 2012).

Although it is intuitive that the presence of herbivores may enhance the diversity of scavenging and parasitic arthropods, field studies showing such patterns are scarce (Barton et al. 2013). Evidence has been presented that a deer carcass can be a hotspot for biodiversity compared to the surrounding forest (Melis et al. 2004) and that the presence of large herbivores can increase tick populations (Keesing et al. 2013), but decrease populations of mice and their fleas (McCauley et al. 2008). For these arthropod groups, human influence may be of extra importance, because in many grazed ecosystems, the resources that these species depend on are highly managed. For instance, removal of carcasses and treatment with anti-parasitic medication are very common in European semi-natural grasslands. Also targeted extermination of livestock parasites has large impacts on parasite populations. For example, the presence of cattle treated with acaricides reduces tick abundance (Keesing et al. 2013), and several species of parasites have been eradicated from parts of their former range (e.g. Wilson 1986, Vreysen et al. 2000). Nevertheless, introductions of livestock outside their native range have probably enhanced the spread of their parasites even more (e.g. Scholl 1993). Anthropogenic causes of changes in large herbivore densities, with in its most dramatic form extinctions of species, will almost certainly lead to co-extinctions of their parasites (Dunn et al. 2009) and scavengers.

In conclusion, the direct effects of large herbivores on arthropod diversity are potentially manifold and sometimes obvious, but are, with the exception of dung beetles, poorly quantified. Nevertheless, the overall impact on arthropod diversity of these direct effects is probably small in comparison to the indirect effects, as we will see in the next sections.

Vegetation-structure mediated effects

The most prominent effect caused by large herbivores is defoliation, leading to a decrease in vegetation height and structural complexity (Fig. 2.3, path 4). Most plants can tolerate defoliation to some extent by resorting to dwarf growth, vegetative spread, or by fast regrowth. Repeated defoliation and trampling can lead to changes in plant species composition (path 3), which will be discussed in section 3.3. For arthropods, short and tall vegetation types provide different abiotic conditions, food resources and predation risk (Fig. 2.3, path 8,9,10). The currently emerging insights how these differences affect arthropod diversity are outlined below.

The abiotic conditions arthropods are exposed to, differ vastly between short and tall vegetation (Fig. 2.3, path 10). When vegetation is permanently grazed short and bare soil is exposed, this often leads to a warmer microclimate in the vegetation and higher soil temperatures, which are essential for the larval development of various thermophilous arthropods such as many grasshopper and butterfly species (e.g. Thomas et al. 1986, Cherrill and Brown 1992, Bourn and Thomas 2002, Roy and Thomas 2003). Moreover, several species require bare, exposed soil for egg deposition (e.g. tiger beetles) or nesting (e.g. solitary bees). Tall and dense vegetation, on the other hand, can act as a temperature buffer, with relatively cool temperatures during the day and benign temperatures at night or in winter (Luff 1966, Dennis et al. 1994), or provide shelter from extreme climatic conditions such as droughts or (periodical) floods (Pétillon et al., 2008). It also offers complex three-dimensional structures for web-building spiders (Gibson et al. 1992b), for species that pupate (many parasitoid Hymenoptera) or deposit eggs (e.g. some grasshopper species) in or on plants, and offers hiding and stalking opportunities for predatory arthropods in the canopy (e.g. crab spiders, praying mantes).

Resource availability also differs between tall and short vegetation (Fig. 2.3 path 9). Tall vegetation possesses aerial structures, like flowers and stems, and the removal of these structures is logically detrimental to their consumers, such as pollinators (Gomez 2003) and insects developing in flower heads and fruits (Morris 1967, 1971, Völkl et al. 1993, Gómez and González-Megías 2007). Tall, ungrazed, vegetation is usually also accompanied by a dense litter layer, providing food for detritivores and their predators. Large herbivores consume large quantities of plant biomass that will therefore not enter the detrital food-web. Litter additions have indeed been shown to increase abundance of predatory arthropods (Langellotto and Denno 2004).

Conversely, short-grazed vegetation offers resources in the form of short-statured plants, that many specialised herbivorous insects depend upon (Thomas et al., 1986; Van Klink et al., in press), but also in the form of nutrient-rich regrowth. After defoliation, the young leaves often have higher nutrient contents than older plant parts (McNaughton 1976, Ydenberg and Prins 1981). All else being equal, herbivorous insects react positively to an increase in resource quality (White 1993, Ritchie 2000), which sometimes leads to species attaining plague densities (Onsager 2000). Positive effects on arthropod diversity, however, have thus far not been shown. Other plant species, especially in dry, unproductive systems, respond to defoliation by producing secondary compounds that are unattractive to large herbivores, but usually also for herbivorous arthropods (Vicari and Bazely 1993, Nykanen and Koricheva 2004). Specialist arthropods, however, have often co-evolved with their host plants in such a way that they tolerate or even profit from the secondary compounds that are produced after defoliation by large herbivores (Poelman et al. 2009).

Furthermore, predation risk is modulated by vegetation height (Fig. 2.3, path 8). Large-eyed predators, such as some ground beetle species (Morris 2000), but also vertebrate predators, such as birds (Belovsky et al. 1990), hunt more efficiently in short vegetation or on bare ground. Tall vegetation may thus protect arthropods from predation, although the densities of arthropod predators, such as spiders, are known to increase with vegetation complexity (Langellotto and Denno 2004).

Taken together, tall, complex vegetation should generally provide more food resources (Lawton 1983), lower predation risk (Belovsky et al. 1990) and more opportunities for coexistence of arthropods than short vegetation, for instance through vertical niche differentiation (Denno 1980). Indeed, a positive relation between vegetation biomass and arthropod diversity is often reported (Duffey, 1962; Luff, 1966; Woodcock et al., 2007; but see Joern, 2005; Woodcock & Pywell, 2009). Consequently, arthropod diversity has often been found to decrease with increasing densities of large herbivores (Dennis et al. 1997, Kruess and Tscharntke 2002a, 2002b, Pöyry et al. 2004). Some arthropod species, however, depend on short vegetation with patches of bare soil (e.g. Joern and Lawlor 1981). It is therefore likely that heterogeneous vegetation, consisting of a patchwork of short and tall vegetation should generally harbour the highest arthropod diversity.

Large herbivores can, under specific circumstances, enhance vegetation heterogeneity. They are usually not distributed homogeneously over the landscape, and exhibit spatial selectivity in their behaviour, such as feeding, defaecation and wallowing (dust-bathing, which creates sparsely vegetated patches (Collins and Barber 1985)). Spatial heterogeneity in feeding behaviour can lead to a patchy vegetation structure of short and tall vegetation if (1) herbivores forage selectively, with smaller herbivore species usually being more selective than large species (Jarman 1974), (2) herbivore density is too low to consume all vegetation and (3) there is a positive feedback between large herbivores and the quality of their food (Adler, Raff & Lauenroth, 2001). Resulting heterogeneity in vegetation structure can then lead to heterogeneity of other ecosystem processes (McNaughton 1984, Hobbs 1996). This is most likely to occur in productive ecosystems (Hobbs and Swift 1988). Conversely, if these conditions are not met, or when high underlying abiotic heterogeneity is already present, grazing is more likely to decrease heterogeneity (Adler et al. 2001).

Although arthropod diversity would be expected to be highest in heterogeneous grasslands, evidence for this relationship is remarkably scarce. Joern (2005) showed a positive relationship between grasshopper diversity and grazing-induced heterogeneity in vegetation height. However, this is not corroborated by other studies searching for such a relationship (Dennis et al. 1998, van Klink et al. 2013). Moreover, some studies report highest vegetation heterogeneity to occur after cessation of grazing, and consequently find highest arthropod diversity under these conditions (e.g. Kruess and Tscharntke 2002a, Pöyry et al. 2006).

To complicate matters, the effects of grazing on vegetation structure vary across spatial scales (WallisDeVries et al. 1999, Adler et al. 2001). Grazing may, for example, lead to a more homogenous vegetation structure at a small scale, while simultaneously leading to heterogeneity at a larger scale (Adler et al. 2001). Such divergent effects of herbivores on vegetation heterogeneity may obscure general effects on arthropods.

Heterogeneity in vegetation structure caused by large herbivores may not only be expressed spatially, temporal heterogeneity is also likely to occur. This may be caused by seasonal variation in plant growth, but also by temporal variation in grazing pressure due to seasonal herbivore migrations or active management (Fryxell and Sinclair 1988, Bischof et al. 2012). The range of spatial and temporal scales at which grazers can affect heterogeneity severely complicates field measurements of the effects on arthropod diversity. An increased understanding of the spatial and temporal scales at which grazing affects vegetation heterogeneity and knowledge of how scale affects the availability of resources and abiotic conditions for arthropods will greatly enhance our understanding of the impact of large herbivores on arthropod diversity.

Vegetation-community mediated effects

Large herbivores often have profound effects on plant diversity (Fig. 2.3, path 3) and plant ecologists have a long history of studying these (Olff and Ritchie 1998). In general, effects of herbivores on plant diversity tend to be positive in wet, productive systems and negative in dry, infertile ones (Olff and Ritchie 1998, Proulx and Mazumder 1998, Bakker et al. 2006, Lezama et al. 2014). Moreover, some of the most plant-species rich ecosystems in the world are traditionally grazed grasslands in Europe (Wilson et al. 2012). A decrease of grazing, therefore often leads to a decrease in plant diversity, as light competition causes exclusion of short-statured plant species (Grime 1973).

Arthropod (consumer) diversity has been hypothesised to be correlated with plant (producer) diversity (Murdoch et al. 1972, Tilman 1986), and experimental increases of plant diversity have indeed been shown to increase arthropod diversity (Siemann et al. 1998, Haddad et al. 2009), abundance (Haddad et al. 2001), functional group richness (Siemann et al. 1998, Rzanny and Voigt 2012) and food-web complexity (Scherber et al. 2010, Rzanny and Voigt 2012). Moreover, this relation was not only found for diversity of herbivorous insects, but also for predators (Haddad et al. 2009) and parasitoids (Ebeling et al. 2012). However, in experimental grazing research this interrelation between plant and arthropod diversity has rarely been supported. In fact, several researchers showed a negative response of arthropod diversity to grazing even when plant diversity increased (Kruess and Tscharntke 2002a, Pöyry et al. 2004), and the generality of these results is corroborated by our quantitative review. The response of plant diversity to grazing therefore seems to be a poor predictor for the response of arthropod diversity.

Obviously, the loss of host plants due to grazing or a lack thereof will lead to the co-extinction of their specialist herbivores. However, the presence of a plant species does not guarantee suitable conditions for its specialist herbivores. This may be due to the presence or absence of certain required plant parts (Morris 1967) or the size of the plant (Lawton 1983), but also to microclimate (Thomas et al. 1986), or isolation from the closest source population (Kruess and Tscharntke 1994). Moreover, tall-statured and widespread plant species generally harbor a richer fauna of specialist insect herbivores than short-statured plant species (Lawton and Schroder 1977, Strong et al. 1984, Tscharntke 1997). This implies that with a lack of grazing, replacement of a short-statured host plant will cause a relatively small loss in diversity, while the gain of tall-statured species can potentially cause a large increase.

Another obvious way by which large herbivores modify the composition of plant communities, is by changing the relative abundance of different plant functional groups (Fig. 2.3, path 3). For instance, in wet, productive systems, grazing can increase the cover of palatable, grazing tolerant plant species (often grasses) (McNaughton 1984), whereas in arid systems it can increase the abundance of unpalatable shrubs (Archer et al. 1995). In temperate systems, both intensive grazing and cessation of grazing can cause an increase in the relative cover of grasses (McNaughton 1986, Milchunas and Lauenroth 1993). Consistent with these observations, polyphagous (grass-feeding) insects have been found to increase under intensive grazing (Nickel and Hildebrandt 2003) as well as after cessation (Littlewood 2008). Similarly, the diversity of both insect-pollinated plants and flower-visiting insects can be affected positively (Vulliamy et al. 2006), negatively (Potts et al. 2009) or not at all (Batáry et al. 2010) by large herbivores. This suggests that shifting abundances of different functional plant groups as a result of grazing can have a large impact on herbivorous and flower-visiting insects and that these shifts may better explain changes in arthropod communities in response to grazing than plant diversity per se.

Soil-mediated effects

Large herbivores can have a strong impact on soil properties, with some of the most consistent outcomes being altered levels of soil nutrients, pH values, water availability (Milchunas and Lauenroth 1993, Bakker et al. 2009) and increased soil compaction (Trimble and Mendel 1995) (Fig. 2.3, path 5). Changes in soil conditions can lead to changes in plant communities (Liddle 1997) (Fig. 2.3 path 6), but can potentially also have direct effects on aboveground arthropods (Fig. 2.3, path 11).

Although the effects of grazing on belowground fauna are strong (Bardgett and Wardle 2003, Beylich et al. 2010), few studies report soil-mediated effects of herbivores on aboveground arthropods. Many species best known for their aboveground appearance, for example clickbeetles and crane flies, spend part of their life cycle below ground, as egg or larva. During these developmental stages, arthropods have been shown to react to changes in soil nutrients (Larsen et al. 1996, Goulet 2003, Oliver et al. 2005), pH (van Straalen and Verhoef 1997, Goulet 2003) and moisture level (Goulet 2003), which can all be altered by large herbivores. Indications that herbivore-mediated changes in soil properties may affect aboveground fauna have so far only been reported for rove beetle communities (Hofmann and Mason 2006) and some ant species (Bestelmeyer and Wiens 2001). The generality of these effects is, however, as of yet poorly known.

Effects on interactions among arthropod species

Like all organisms, co-occurring arthropod species interact in myriad ways, including resource competition, predation and mutualistic interactions (Fig. 2.3, path 15). Food-webs are complex in nature, and often, changes in one trophic level can have unforeseen consequences for another trophic level or guild (Schmitz 2011). Experimental evidence for the way in which large herbivores can alter relations between arthropod species is scarce. It has been suggested that large grazers have an especially negative impact on parasitoids through direct disturbance and fragmentation of resources, thereby shortening arthropod food chains in grazed grasslands (Tscharntke 1997). The general dearth of knowledge on the response of parasitoid Hymenoptera to habitat change (Shaw and Hochberg 2001, Shaw 2006), however, inhibits generalisation, and in fact positive effects of large herbivores on parasitoid abundance in experimental thistle patches have been reported (Vanbergen et al. 2006).

There is, however, a great potential for bottom-up driven diversity control in grasslands, as suggested by the strong relationship between vegetation complexity and arthropod diversity (section 3.2). An increase in abundance or diversity of herbivorous insects and detritivores can potentially increase the diversity of higher trophic levels, as was shown in plant diversity manipulation experiments (e.g. Scherber et al. 2010). From grazing experiments, so far only correlative evidence is available, showing similar changes in the diversity of herbivorous and predatory taxa to changes in grazing pressure (Gibson et al. 1992a, Kruess and Tscharntke 2002b, Báldi et al. 2013). Moreover, the diversity of parasitic Hymenoptera was found to be well correlated to overall diversity (Anderson et al. 2011), suggesting that these potentially respond indirectly to herbivore-mediated changes in diversity of lower trophic levels. Still, causal relations explaining these changes have not yet been mapped in the context of grazing.

There is also potential for changes in top-down processes controlling diversity, since large herbivores can affect the abundance and diversity of predatory arthropods, which then might affect the diversity of lower trophic levels. Evidence for the importance of this process in grasslands is, however, extremely limited, and increased predator abundance may in fact enhance the diversity of lower trophic levels (Sanders and Platner 2007). To better understand these complex relations, there is a strong need for food-web approaches in grazing research, with a good potential for path analysis (e.g. Scherber et al. 2010).

Finally, it is possible that grazing alters competitive outcomes between arthropod species from the same trophic level. For plants, it is well established that grazing strongly alters competitive relationships (Hobbs and Huenneke 1992, Olff and Ritchie 1998), but for arthropods, evidence is scarce. The importance of competitive exclusion in arthropod communities has been debated for decades (Lawton and Hassell 1981, Denno 1995). Although there is now ample evidence that resource competition and competitive exclusion do occur between herbivorous insects (White 1993, Denno 1995, Reitz and Trumble 2002, Kaplan and Denno 2007), it remains unclear how important these processes are in structuring natural communities in a field setting. Since the vast majority of arthropod species exploit different resource bases, the importance of competition among species in limiting diversity is probably small (Strong et al. 1984). Therefore, the disruption of competitive hierarchies by large herbivores is unlikely to have great impacts on arthropod diversity (Fuentes and Jaksic 1988). Disentangling the relative importance of all these processes remains a formidable future challenge.

SYNTHESIS

Why is arthropod diversity so often negatively affected by grazing?

Ultimately, the mechanisms through which large herbivores affect arthropods are mediated by three key main components of arthropod population regulation: predation, trophic resource availability and abiotic conditions (Fig. 2.3). In the presence of large herbivores, (unintentional) predation and direct mortality of arthropods are likely to increase, which is especially likely to affect sedentary arthropods (section 3.1). These direct effects will be negative for diversity if mortality rates are high, but not detrimental if arthropod populations can be maintained.

The total trophic resource availability for arthropods will be reduced as herbivores consume plants and litter, which form the base of the arthropod food-web (section 3.2). Therefore, overall arthropod abundance is likely to be reduced under grazing. Given the large body of theoretical (Fisher et al. 1943) and empirical evidence (Kruess and Tscharntke 2002a, Pöyry et al. 2006) showing a positive relationship between abundance and diversity of organisms, defoliation by large herbivores can be expected to be negative for arthropod diversity. However, plant diversity is often increased by grazing (Olff & Ritchie, 1998), creating opportunities for a wider group of specialist herbivores (section 3.3). Also for species such as dung beetles and parasites resource abundance will increase with grazing (section 3.1).

Large herbivores often strongly modify the abiotic environment experienced by arthropods (section 3.2). Such modifications will be positive for some species and negative for others. Overall effects of changes in microclimatic conditions on diversity therefore depend on the habitat requirements of the species present in the regional species pool and the interactions of large herbivores with prevailing (micro-climatic) conditions.

Taking all these effects together, the variation in biotic (e.g. dung and plant species) and abiotic (e.g. microclimate and habitat complexity) conditions *may* be enhanced by large herbivores (sections 3). Therefore, arthropod diversity *can* be augmented by large herbivores if the following conditions are met: 1) grazing causes an increase in biotic and abiotic heterogeneity, 2) this increase in heterogeneity occurs at such a spatial and temporal scale that it can be exploited by new species immigrating from the regional species pool and 3) this positive effect of increased heterogeneity is large enough to compensate for the negative effects of direct mortality and resource competition between arthropods and large herbivores. This combination of conditions is most likely to occur at low densities of herbivores, because direct mortality and resource competition are minimal, while variation in (a)biotic conditions is most likely to increase (see section 3.2).

High densities of large herbivores are likely to always be detrimental to arthropod diversity, although some arthropod species or groups may profit. This is indeed supported by most empirical studies (e.g. Gibson et al. 1992a, Kruess and Tscharntke 2002a, 2002b, Nickel and Hildebrandt 2003, Rickert et al. 2012). Studies reporting otherwise (Vulliamy, Potts, & Willmer, 2006; Yoshihara et al., 2008) have all studied flower-visiting insects, which may not spend their whole life-cycle in the study environment and may not represent overall arthropod diversity (Vessby et al. 2002, Oertli et al. 2005).

Why is arthropod diversity affected more negatively by grazing than plant diversity?

The difference between plants and arthropods in response to grazing can be understood by considering the mechanisms by which both groups are affected. Three differences between plants and arthropods emerge to explain the contrasting response to grazing.

First, plant diversity is generally increased by grazing through a decrease in light competition, and an increase in colonisation by new species (Olff and Ritchie 1998). Since there is no evidence for an important role of competition in limiting arthropod diversity (section 3.5), it is unlikely that large herbivores can cause any type of competitive release on arthropod communities. Conversely, the majority of species at the base of the arthropod food-web (herbivores and detritivores) compete directly for resources with large herbivores, as outlined in the previous section. This competition is highly asymmetrical, and can lead to competitive exclusion and decreased population sizes (Gómez and González-Megías 2002), which is likely to reduce arthropod diversity.

Secondly, the habitat requirements of plants and arthropods operate at different spatial and temporal scales (Bourn and Thomas 2002). Plants are sedentary and need a specific set of conditions that are all met at one spot. Arthropods generally have distinct phases in their life-cycle, which often need different site conditions (e.g. warm microclimate and abundant host plants for larval development and nectar for adult life-stages). In particular at immature stages insects have a narrow niche and limited dispersal ability to actively find suitable habitat patches (Bourn and Thomas 2002). For arthropods to survive, the requirements of all life-cycle stages must be met within the area the species can travel. This means that single arthropod species often need a certain level of habitat heterogeneity (creating favourable microclimatic conditions and food resources for all life stages) at a specific spatial scale to survive. Plant species, on the contrary, can thrive in fairly homogeneous grasslands as long as their specific habitat requirements are met. As more intensive grazing management generally decreases habitat heterogeneity (see section 3.2) this is inevitably detrimental to many arthropod species, even if the requirements of individual life stages are still met. In addition, the life-cycle of many arthropod species is strictly synchronised (Zaslavski 1988). This means that the habitat conditions for each life-cycle stage must be present at exactly the right time of year, making arthropods especially sensitive to the timing of grazing (Carvell 2002, Lenoir and Lennartsson 2010, van Noordwijk et al. 2012).

Third, plants are more plastic in their response to grazing than arthropods are. Plants can often survive (periodical) high trampling and defoliation through dwarf growth, vegetative spread and belowground storage of resources. Arthropods generally do not have such back-up strategies. Some arthropods can attempt to escape unfavourable conditions by dispersal (Berggren 2004), but they can only disperse over limited distances where they have to find favourable conditions again. This difference in vulnerability to grazing between plants and arthropods has strong implications for nature conservation.

Implications for arthropod conservation management

Most grassland types worldwide depend on the presence of large herbivores to prevent succession to scrub or forest (Hobbs and Huenneke 1992). In most of these grasslands herbivore densities are (strongly) influenced by human intervention including active management, exploitation, agricultural activities and abandonment of former agricultural practices. This will have profound impacts on these grasslands and their biodiversity, including arthropod diversity. Conservation goals, and hence decisions on stocking densities and other human interventions, vary widely over grazed ecosystems. A major part of grazed systems is being used for livestock grazing, where production of meat or other animal products, rather than nature conservation, is the primary goal. In a much smaller area of global grasslands, conservation purposes prevail. Here, management priorities may vary from a focus on maintaining diverse herbivore assemblages in African savannahs (Mbano et al. 1995), to the restoration of natural processes on the North American prairies (Sanderson et al. 2008) and a focus on preserving high (plant) diversity in European semi-natural grasslands (WallisDeVries 1998, Ostermann 1998). In agricultural grazing systems, management effects on (arthropod) diversity are generally not considered in decision making. Indeed, studies investigating the effects of livestock grazing in agricultural systems usually report negative impacts on diversity (Smith 1940, Forbes et al. 2005, Xie et al. 2008) and abundances (Hutchinson and King 1980) of arthropods. Also in natural and semi-natural grasslands, arthropods are not always given high priority, but awareness of the importance of arthropods is growing among conservationists, as is attention for arthropods in conservation and restoration research (Fig. 2.1E). Our review highlights that specific attention for arthropods is essential for their conservation, as arthropods are generally more sensitive to grazing than plants. Therefore we highly recommend that arthropod species richness is monitored in addition to botanical composition when evaluating grazing management.

Although grazing is essential to conserve species-rich grasslands on the long run, we have shown that increased grazing intensity quickly becomes detrimental to overall arthropod diversity. On the other hand, high plant species richness is often best attained under moderate grazing regimes (Olff and Ritchie 1998, Wilson et al. 2012) and many thermophilous insects, including many butterflies depend on favourable microclimates (Bourn and Thomas 2002) created by more intensive grazing (see section 3.2). Both plants and thermophilous butterflies characteristic of semi-natural grasslands have become severely threatened due to increased eutrophication and abandonment of traditional farming practices (Ostermann 1998, Van Swaay et al. 2010) and, hence, are of special conservation interest (Van Swaay et al. 2010). This creates potential for conflict between the requirements of plant diversity, threatened arthropod species and maintenance of high overall arthropod diversity (see for example Negro et al. 2013). In habitat restoration, where arthropod populations of high conservation value are absent, a focus on plant restoration in the first few years may be justified, as this is a prerequisite for the establishment of many arthropod species (Woodcock et al. 2010, 2012). However, in a conservation context, solutions should be sought to meet the requirements of as many species as possible by conserving or promoting a heterogeneous habitat. Low densities of herbivores provide the best chance of attaining this objective (see section 4.1), but so far no evidence has been presented that a single management regime can accommodate all species in a local species pool (Dennis et al., 1997, Dennis, Young & Bentley, 2001). Therefore, it has been suggested that arthropod diversity can best be conserved at the landscape scale by maintaining grasslands under different types of management in close proximity (Dennis et al. 1997, Morris 2000, Kruess and Tscharntke 2002b, Rickert et al. 2012). In addition to such spatial variation, temporal heterogeneity can be created by using rotational grazing with periods (weeks to decades) of grazing alternated with periods of cessation. This creates periods in which the negative effects of grazing (direct mortality and resource competition) are absent (Morris 1967), while still providing opportunities for high plant diversity and an open vegetation structure. Rotational grazing has been shown to be successful for arthropod conservation in several ecosystems (Morris et al. 2005, Farruggia et al. 2012), but needs additional research in many others. Especially the duration of the different rotations may be of importance, since several weeks of grazing exclusion may already benefit flower-visiting insects (Farruggia et al. 2012), but endophagous grass-feeders may require multiple years before their populations increase (Rothenwöhrer et al. 2013). Offering variation in grazing intensity and timing on a landscape scale may also offer a feasible approach to increase arthropod diversity in agricultural landscapes, especially where agricultural fields are interspersed with semi-natural habitats (Tscharntke et al. 2012).

Whether specific species survive under a given grazing regime inevitably depends on the match between their habitat requirements and the timing, scale and intensity of grazing. While low intensity grazing and variation of grazing intensities at the landscape scale will benefit overall arthropod diversity, more detailed grazing regimes will be required in cases where a specific suite of target species has been set. In these cases, a fruitful approach to finding the optimal grazing regime is to analyse the life-cycles of these species (Williams et al. 2010, Verberk et al. 2013). This approach has been advocated for conservation purposes (van Noordwijk et al. 2012), but can also be used to actively suppress populations of pest species (Onsager 2000).

NEXT STEPS

From this review, clear patterns explaining the patterns of arthropod diversity in grazed ecosystems have emerged. Analysing the mechanisms affecting arthropod diversity responses to grazing has revealed why generally arthropod diversity responds negatively to (intensive) grazing and how the variation in these responses can be explained. Our study has also identified a number of issues that remain poorly understood and require further research. Although we have argued that a positive effect of large herbivores on arthropod diversity can mostly be expected at low herbivore densities, empirical evidence remains scarce, and more experimental testing is needed. In particular we need to expand our knowledge of the specific conditions under which large herbivores have a positive effect on arthropod diversity, for example by directly comparing a number of promising low intensity grazing regimes. As we have demonstrated that spatial and temporal heterogeneity in (a)biotic conditions are crucial to arthropod diversity, these aspects need special attention. It has become apparent that there are large differences between arthropod taxa in their response to grazing. Therefore, multi-taxon studies are highly desirable, preferably conducted over multiple years to account for weather effects and population dynamics. In addition, a great deal can be learnt from smaller experimental studies targeting single mechanisms (e.g. incidental ingestion, effects of soil compaction or effects of plant diversity). To add to our current knowledge, these experiments should especially focus on effects of these mechanisms at the community level (the extent to which diversity and composition are affected). Helpful approaches in this respect include 1) trait-based approaches, demonstrating which traits determine to what extent arthropod species are affected by certain mechanisms and 2) integrated food-web studies, demonstrating the importance of bottom-up, top-down and competitive interactions in shaping arthropod communities in grazed ecosystems. A food-web approach could also be used to link above- and belowground effects of large herbivores. Finally, to understand differences in responses of arthropod diversity to grazing between ecosystems, it is important to be able to compare in situ grazing pressure between studies and ecosystems. Such comparisons are currently hampered by, for example differences in ecosystem productivity and land-use history. An account of the percentage net primary productivity consumed by large herbivores should improve comparability, and aid future syntheses.

CONCLUSIONS

1) The vast majority of published studies on the effects of grazing on arthropods were conducted in Europe and North America, and focus on a small number of arthropod taxa. Studies demonstrating effects on overall arthropod diversity are virtually lacking.

2) Responses of arthropod diversity to grazing are highly variable, but arthropod diversity is often more negatively affected than plant diversity. Moreover, plant diversity is a poor predictor for arthropod diversity in grazed ecosystems. Therefore, we strongly recommend considering the specific requirements of arthropods and including arthropods in monitoring schemes evaluating the effects of grazing.

3) Unintentional predation and disturbance have a negative effect on population sizes and diversity of most arthropod groups. Positive direct effects, like availability of resources such as dung and carrion, will only benefit a small number of arthropod species.

4) Defoliation by large herbivores will cause a reduction of resource abundance for the base of the arthropod food-web (herbivores and detritivores) and also reduces habitable space for species dependent on tall vegetation structures. This will generally have a negative effect on diversity.

5) Large herbivores can under specific conditions increase both plant diversity and structural heterogeneity of the vegetation. This increase in resource heterogeneity may increase arthropod diversity, but only if its positive effects are large enough to compensate for the above-mentioned negative effects of large herbivores, outlined above.

6) Conservation strategies aiming at maximising heterogeneity, such as low intensity grazing, maintenance of different types of management in close proximity, or rotational grazing regimes, are most likely to conserve or restore arthropod diversity.
The online supporing information to this article can be found at …

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Chapter 3

Contrasting responses of the diversity of arthropod habitat specialists and generalists to salt-marsh elevation and livestock grazing

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ABSTRACT

Ecological theory suggests that with increasing environmental adversity, species richness (α-diversity) and compositional variability between samples (β-diversity) should decrease, as only those species that are adapted to these harsh conditions will remain. This has, however, rarely been tested in field settings where multiple types of biotic and abiotic stress might interact.

We tested the hypotheses that with increasing inundation frequency on a salt-marsh elevation gradient α- and β-diversity of salt-marsh arthropods would decrease, and that biotic stress induced by livestock grazing would enhance environmental adversity, as protective vegetation cover is removed, leading to a steeper α-diversity decline and a decrease in β-diversity. We tested these hypotheses on the community of carnivorous ground-dwelling arthropods on two salt marshes bordering the Dutch Wadden Sea.

We found general support for these hypotheses, but found opposite responses of communities of habitat specialists and habitat generalists, and large variation between the sites. Habitat generalists generally responded in accordance with our hypotheses, although under the most adverse conditions (grazed low marsh) β-diversity was increased due to low α-diversity. Habitat specialists, however, showed highest α- and β-diversity on the ungrazed low marsh, suggesting that here other processes than environmental filtering determine their community composition. Under grazed conditions, their β-diversity peaked where α-diversity, for unexplained reasons, was lowest. These results indicate that when testing community assembly theory in a field setting, species specialised on adverse conditions can obscure patterns in α- and β-diversity, and that good knowledge on habitat affiliations can aid understanding these patterns.

Submitted

INTRODUCTION

Identifying and understanding processes that shape ecological communities is one of the key goals in community ecology. It is now well established that communities are shaped by both deterministic factors, as defined by the ecological niches of its species, and by stochastic factors such as population dynamics, colonisation and extinction (Cottenie 2005, Leibold and McPeek 2006, Thompson and Townsend 2006, Lindo et al. 2008, Ellwood et al. 2009, Caruso et al. 2012). Which factors influence the relative importance of either process under different ecological conditions is, however, less clear.

Ecological theory suggests that under benign conditions, stochastic processes are the most important structuring forces in community assembly, because all species of the local species pool can potentially occur, and competition, extinction and immigration influence the final composition of the community (Chase 2007). Therefore, composition of samples taken under benign conditions would be expected to be dissimilar, indicated by high β-diversity (Whittaker 1960). Under adverse environmental conditions, however, environmental filtering dictates which species are able to persist, emphasising deterministic processes (Chase 2007). Hence, under these harsh conditions, samples should be compositionally similar, indicated by low β-diversity (Chase 2007). Over the past decade it was indeed shown that different types of environmental adversity affect community assembly: stochasticity in community assembly increases with productivity (Chase 2010), while it decreases under drought (Chase 2007), predation (Chase et al. 2009) or disturbance (Lepori and Malmqvist 2009). Only rarely have these ideas been tested along natural gradients of adversity and research on the classical gradients, such as latitudinal and altitudinal gradients, has yielded controversial results (Qian and Ricklefs 2007, Kraft 2011, Qian et al. 2013). Under natural conditions interactions between different types of environmental adversity may occur, with possible synergistic effects on communities (Hobbs 2001, Travis 2003, Bogich et al. 2012).

In our study system, coastal salt marshes, a gradient of environmental adversity is induced by frequency of inundation by sea water. On lower parts of the gradient, inundations occur more frequently than on higher parts, creating a combined gradient of increasing disturbance, frequency of anoxic conditions and salt concentrations in the soil and food chain (Cheng 1976, Adam 1990). Plant communities are species-poor and generally consist of halophytic (sub-) species, whereas arthropod communities mainly consist of habitat specialists and extreme ubiquists (Foster and Treherne 1976). Species distributions are strongly associated with the environmental gradient, which leads to a zonation in species composition of both plants and arthropods and an increase in species richness with elevation (Beeftink 1977, Irmler et al. 2002, Finch et al. 2007, Pétillon et al. 2008).

An additional factor affecting the plants and animals on salt marshes is livestock grazing. On Western European salt marshes, livestock grazing has been common practice for agricultural purposes for millennia (Bazelmans et al. 2012), and is currently still performed for reasons of nature conservation, coastal protection or agriculture in several countries (Esselink et al. 2009). Grazing prevents succession to botanically species-poor, homogeneous tall vegetation and maintains a botanically richer short sward through disturbance, biomass removal and abiotic changes (Bakker 1985, Esselink et al. 2002, Schrama et al. 2013a).

Many arthropod species respond negatively to livestock grazing (Irmler and Heydemann 1986, Pétillon et al. 2007, Ford et al. 2013), but some species are more abundant in grazed than in ungrazed marshes (Irmler and Heydemann 1986, Pétillon et al. 2007, Ford et al. 2013). Arthropod species richness is thus normally higher in ungrazed salt marshes (Andresen et al. 1990, Pétillon et al. 2007), and for carnivorous species this was shown to be partly attributable to the increased occurrence of non-coastal and common species rather than salt-marsh specialists after the encroachment of the tall grass *Elytrigia atherica* (Andresen et al. 1990, Pétillon et al. 2005). The effects of grazing and surface elevation on arthropod communities have so far mainly been studied separately, although it is likely that interactive effects occur. For example, grazing does not only cause direct mortality to salt marsh arthropods by trampling, ingestion or removal of host plants, but also indirectly increases the effects of inundations on arthropods by removal of protective vegetation cover. We, therefore, expect that species richness (α-diversity) will decrease more strongly with decreasing marsh elevation, as a proxy for environmental adversity, under grazing than in the absence of grazing. Moreover, we expect β-diversity to decrease with decreasing marsh elevation, and will be lower under grazing, because of the increased exposure to adverse conditions. These predictions might differ between species restricted to salt marshes and ubiquitous species, as these are known to respond differently to typical salt-marsh conditions (Hemminga and Van Soelen 1988, 1992, Moon and Stiling 2002b, Pétillon et al. 2008) (summarised in Table 3.1). We test these expectations on the community of ground-dwelling carnivorous arthropods (spiders, ground beetles and shore bugs) on two salt marshes along the Dutch Wadden Sea. Carnivorous arthropods are not associated with specific plant communities, but respond strongly to physical changes of their habitat (e.g. Duffey 1962, Luff 1966), and are therefore well suited to test these predictions.

Table 3.1 Summarised hypotheses of the effects of surface elevation and grazing on α- and β-diversity of ground-dwelling arthropods on salt marshes. Hypotheses are given for all species combined, habitat specialists (salt-marsh species) and non-specialists (ubiquitous species and species with other habitat affiliations (some species typical for dune and moist habitats)).

		elevation decrease (increase in adversity)	grazing
all species	α-diversity	-	+/-
	β-diversity	-	-
habitat specialists	α-diversity	+	+
	β-diversity	?	?
habitat generalists	α-diversity	-	-
	β-diversity	?	?

METHODS

Study area and site characteristics

This research was conducted on two salt marshes along the Dutch Wadden Sea coast, a mainland salt marsh (Noord Friesland Buitendijks (NFB hereafter), 53°20′N; 05°43′E) and an island marsh (Schiermonnikoog, 53°28′N, 06°13′E) (Fig. 1.2). Both sites have been under summer grazing (May – October) with a grazing pressure of approximately one cow per two hectare for at least the past decade.

The mainland site (NFB) was established from sedimentation fields for land reclamation works during the first half of the 20th century, but is now under nature protection. Its soil consists of several metres of marine clay and on the landward side, the salt marsh is bordered by a seawall, behind which intensive agriculture is the dominant land-use type. The grazed and ungrazed salt marshes are separated by a permanently flooded ditch.

The island of Schiermonnikoog is located 8 km from the mainland coast, with a large natural salt marsh. Its soil consists of several decimetres of clay on sand. Grazing at this site was established in 1992, while the ungrazed treatment was abandoned in the late 1950s. The salt marsh gradually transitions into a coastal dune system.

At both sites, fresh water supply for livestock was located on the high marsh, several hundred meters from our experimental plots. The ungrazed marshes at both sites were dominated by the tall, coarse grass *Elytrigia atherica* at higher elevations, and by tall perennial or annual forbs on the low marsh (Table 3.2). The grazed marshes at both sites were characterised by short vegetation (<8cm), dominated by several species of grazing tolerant grasses and short statured forbs (Table 3.2).

At the island site, the typical lower salt-marsh plant community was located at lower elevations than at the mainland site. This can probably be attributed to the fact that maintenance of drainage ditches was abandoned at the mainland site in 1990, whereas the island site has a well-developed natural creek system. A lack of drainage causes waterlogging and consequentially disfavours plant species typical for higher salt marshes that depend on well aerated soils (Armstrong et al. 1985, Davy et al. 2011). Differences between the sites are summarised in Table 3.2 and 3.3. Despite the differences between the sites, ecological processes structuring arthropod communities should be similar because of the similarity in environmental gradients.

Table 3.2 Dominant plant species on the different elevation zones under grazed and ungrazed conditions on the salt marshes of Noord Friesland Buitendijks (NFB) and Schiermonnikoog.

	Mainland (NFB)		**Island (Schiermonnikoog)**	
	Grazed	Ungrazed	Grazed	Ungrazed
High marsh	*Agrostis stolonifera*	*Elytrigia atherica*	*Festuca rubra*	*Elytrigia atherica*
Low marsh	*Puccinellia maritima*	*Aster tripolium & Atriplex prostrata*	*Puccinellia maritima*	*Atriplex portulacoides*

Study design

At both sites we established a sampling area of approximately 1 km in length, covering an elevational gradient from the higher salt marsh to the lower marsh on both grazed and ungrazed marshes. At the mainland site, the gradient spanned 45 cm, from 70 to 35cm above mean high tide (+MHT) and at the island site 60 cm, from 70 to 10 cm +MHT, corresponding to the distribution of higher marsh and lower marsh vegetation (Table 3.3). We did not extend our studies into the pioneer zone because livestock was excluded from this area.

On both the grazed and the ungrazed marshes, we established four sampling plots along each gradient, two plots in high-marsh vegetation and two plots in low-marsh vegetation (Fig. 3.1). Plots were spaced at least 100 m apart and were established at positions that were relatively homogeneous in elevation. There was at least 10 cm elevational differ-

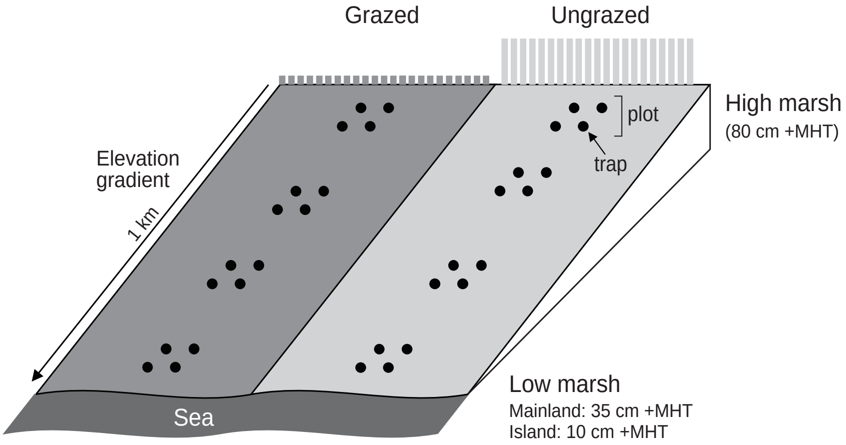

Figure 3.1 Schematic representation of the experimental setup for trapping carnivorous ground dwelling arthropods on the grazed and ungrazed treatments on two sites.

Table 3.3 Summarised differences between sites.

	Mainland (NFB)	**Island (Schiermonnikoog)**
Origin	Sedimentation fields	Natural
Hinterland	Agricultural	Coastal dunes (protected)
Start of low marsh (*P. maritima*)	+40 cm MHT	+ 10 cm MHT
Soil	Heavy clay (>1m)	Clay on sand (cm)
Diversity (expected)	Low	High
Elevational gradient	145 – 180 cm	120 – 180 cm
Inundation frequency lowest elevation (10 yr mean)	60.6 yr^{-1}	195 yr^{-1}
Sedimentation rate	High (>10mm yr^{-1})	Low (<5mm yr^{-1})

ence between plots, thus creating an elevational gradient of 35 cm at the mainland and 60 cm at the island site.

At each plot, we placed four pitfall traps (Ø 11cm). Traps were spaced at least ten metres apart, which is considered the minimum distance at which traps will not influence each other (Ward et al. 2001). They were covered by sturdy plastic roofs to protect them from rain, trampling and evaporation. Traps were filled with a 4% formaldehyde solution as preservative. After collection, invertebrates were stored in 70% alcohol until identification.

Arthropods were trapped during three one-week periods in the summer of 2009 (May, June/July, August) and the three samples from each trap were pooled. We identified three groups of carnivorous arthropods that are common on salt marshes to species level: ground beetles following Boeken et al. (2002), spiders following Roberts (1987) and shore bugs following Cobben (1960).

Statistical analysis

First, we visualised differences between grazing treatments using non-metric multidimensional scaling (NMDS) of Morisita-Horn dissimilarities using the Vegan package (Oksanen et al. 2013). The variable surface elevation was correlated with the NMDS axes and plotted in the graphs. All statistical analyses were done using R 3.0.2 (R Core Team 2013).

In order to understand the drivers of patterns in α- and β-diversity of all species, we studied the effects of grazing and elevation on the complete species pool and two subsets of species: habitat specialists and habitat generalists. Species confined to saline habitats were classified ‘specialists’, whereas species occurring in a broad range of habitats, or had habitat associations other than with salt marshes (mostly sand dunes or wet habitats) were classified ‘generalists’. This classification was based on Turin (2000) for ground beetles, Hänggi et al. (1995) for spiders and Cobben (1960) for shore bugs.

α-diversity

Differences in arthropod α-diversity (total number of species per trap) between treatments and along the elevational gradient were tested using generalised linear models (GLM) with Poisson distributions. Grazing, elevation, and their interaction were entered as factorial variables and backward model selection was applied. When elevation was a significant factor, we tested for differences between levels with Tukey tests (linear hypotheses). However, when the interaction between grazing and elevation was significant, we applied separate Tukey tests for the grazed and ungrazed treatments and differences in grazing effects were assessed for each elevational level separately. To test for differences in overall α-diversity along the entire gradient, we used a generalised linear mixed modelling (GLMM (Bates et al. 2013)) where elevation was used as random factor.

β-diversity

For measuring variation in species composition between traps, we calculated Morisita–Horn dissimilarities between all pairs of traps at each site using the Vegan R-package

(Oksanen et al. 2013). This metric of dissimilarity is based not only on differences in the presence or absence of species, but also takes differences in species abundances into account, and is highly robust against under-sampling (Beck et al. 2013).

We used the 'Betadispersion' method recently published (Bacaro et al. 2011, 2013) to test for differences in β-diversity between treatments and elevational levels. This method was designed to test differences in β-diversity between groups of plots based on pairwise dissimilarities, and uses a permutation approach to derive a test-statistic (Bacaro et al. 2011). We first tested for differences between elevational levels for each treatment separately. Differences between elevational levels were again assessed using Tukey tests. Secondly, we tested for differences between grazed and ungrazed marshes, both using the complete dataset along the entire elevational gradient for each site and for each elevational level separately. When significant differences were found, we tested for effects at each elevational level, again using Tukey tests.

RESULTS

In total we caught 12,879 individuals of 89 species at the two sites. As expected, the island marsh of Schiermonnikoog was richer in species (75 species) than the mainland marsh of NFB (45 species). Spiders were represented by 52 species on the island marsh and 30 species on the mainland marsh, ground beetles by 19 species on the island and 14 on the mainland, and four species of shore bugs were found on the island versus only one species on the mainland salt marsh (Appendix 3.1). All but one of the ground beetle species and all shore bug species recorded are known as good dispersers with fully winged individuals and regular flight observations (Cobben 1960, Turin 2000). Regarding the recorded spider species, dispersal characteristics of habitat specialists are mostly unknown (except for

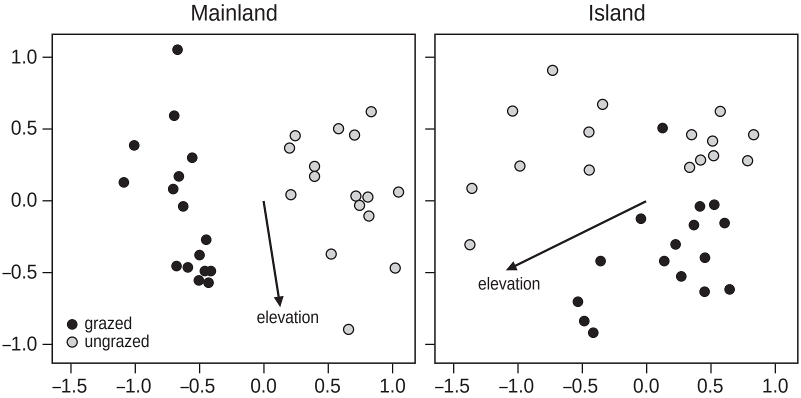

Figure 3.2 NMDS biplots of Morisita-Horn dissimilarities of communities of ground-dwelling carnivorous arthropods (spiders, ground beetles and shore bugs) at two salt marsh sites at the Dutch Wadden Sea coast. Animals were caught using pitfall traps positioned along an elevational gradient under grazed and ungrazed conditions. Elevation was fitted to the dissimilarity matrix by correlation.

regular ballooning of *Pardosa purbeckensis* (Bonte et al. 2007)), but most habitat generalist species have been observed to balloon frequently (Bonte et al. 2003, Thomas et al. 2003), and all species belonged to families with observed ballooning behaviour (Bell et al. 2005).

The communities of the grazed and ungrazed marshes differed considerably according to NMDS (Fig. 3.2) and elevation had a strong correlation with the NMDS axes at both sites (mainland: $R^2 = 0.69$, $p = 0.001$; island: $R^2 = 0.82$, $p = 0.001$; Fig. 3.2). The most abundant species on the grazed marshes was the halophilic spider *Erigone longipalpis*, making up 47% and 42% of all individuals at the mainland and the island respectively. In the ungrazed marshes, the wolfspider *Pardosa purbeckensis* made up 71% of all individuals at the mainland site, and 23% at the island site. Only *Praestigia duffeyi* was more abundant at the ungrazed island site, making up 27% of all individuals.

α-diversity

The effects of surface elevation on arthropod α-diversity differed somewhat over the two sites. Only at the mainland site under grazing, α-diversity of all species decreased with elevation (Table 3.4, Fig. 3.3A), whereas at the island site no significant differences were found at all (Table 3.4, Fig. 3.3D). At the mainland site, this decrease was explained by the decrease in α-diversity of habitat generalists under grazing (Fig. 3.3B), whereas diversity of specialists was not affected (Fig. 3.3C). At the island site, α-diversity of habitat generalists decreased with elevation in both the grazed and ungrazed marshes (Table 3.4, Fig. 3.3E). Habitat specialists showed no significant response under grazing, but their α-diversity increased as elevation decreased in the absence of grazing (Fig. 3.3F).

Table 3.4 Summary statistics of the effect of elevation on α- and β-diversity of ground-dwelling arthropods on grazed and ungrazed salt marshes. Models for α-diversity are based on Poisson distributed GLM's and models for β-diversity are based on average pairwise comparisons between traps (Morisita-Horn index), which were assessed for significance using a permuational approach (β-dispersion method; Bacaro et al. 2011). For a visual representation see Fig. 3.3 and 3.4.

		all species		**habitat generalists**		**habitat specialists**	
Mainland							
α-diversity	grazed	$\chi^2 = 23.03$	**<0.001**	$\chi^2 = 30.52$	**<0.001**	$\chi^2 = 5.00$	0.65
	ungrazed	$\chi^2 = 0.46$	0.93	$\chi^2 = 0.47$	0.93	$\chi^2 = 5.00$	0.65
β-diversity	grazed	F = 20.95	0.12	F = 50.83	**0.006**	F = 39.2	0.046
	ungrazed	F = 94.43	**0.001**	F = 26.94	0.06	F = 12.02	**0.001**
Island							
α-diversity	grazed	$\chi^2 = 9.86$	0.20	$\chi^2 = 27.8$	**<0.001**	$\chi^2 = 6.11$	0.11
	ungrazed	$\chi^2 = 9.86$	0.20	$\chi^2 = 27.8$	**<0.001**	$\chi^2 = 32.92$	**<0.001**
β-diversity	grazed	F = 3.15	**0.049**	F = 89.59	**0.002**	F = 12.46	**0.001**
	ungrazed	F = 82.39	**0.002**	F = 17.65	**0.001**	F = 62.53	**0.007**

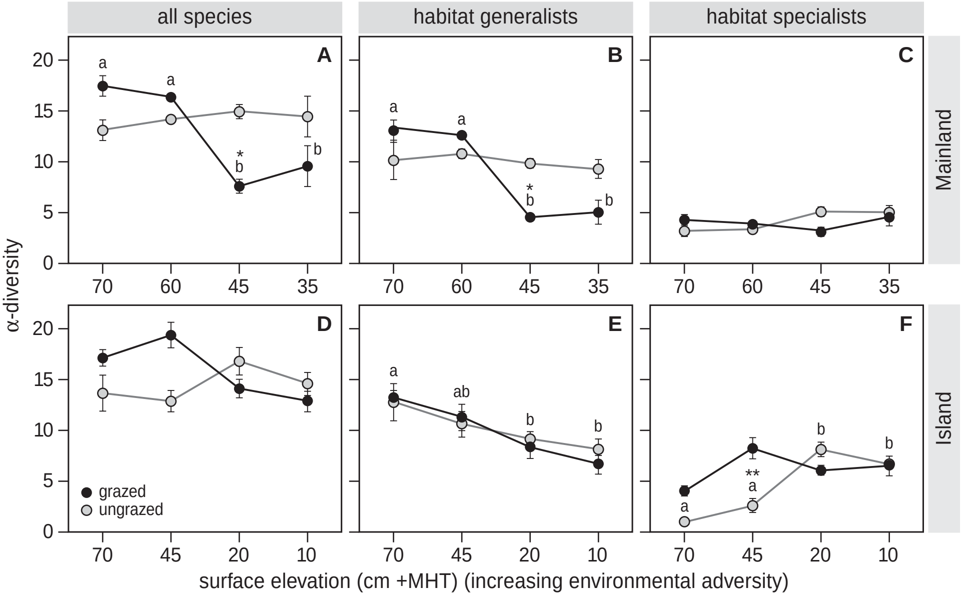

Figure 3.3 Effects of surface elevation and grazing management on arthropod α-diversity at two salt marshes. Different letters indicate significant differences between elevational levels, * indicates significant differences between grazing treatments at individual elevational levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Error bars represent standard errors. For summary statistics see Table 3.4.

Grazing, by contrast, had few significant effects on α-diversity. Overall α-diversity per trap along the entire gradient did not differ between treatments at either site (Table 3.5). At the island significantly more habitat specialist species were trapped under grazing than under ungrazed conditions, but this was not the case at the mainland site, nor did habitat generalists differ in α-diversity between treatments (Table 3.5).

When comparing the effects of grazing at each elevational level, few significant differences became apparent. At the mainland site at 45 cm +MHT, α-diversity was significantly higher at the ungrazed marsh (Tukey's test, $p = 0.03$, Fig. 3.3A), which was caused by a decrease of habitat generalists (Tukey's test, $p = 0.03$, Fig. 3.3B). At the island site, overall α-diversity was not affected by grazing at any elevational level, but α-diversity of habitat specialists was higher at 45 cm +MHT under grazing. No significant differences between grazing treatments were found at other elevational levels, or for habitat generalists (Fig. 3.3F).

β-diversity

We found significant differences in β-diversity over the elevational levels, but these differed between grazing treatments. For the whole species pool, at both sites there was a general decrease in β-diversity only under ungrazed conditions (Table 3.4, Fig. 3.4A,D). Under grazing no significant effect was found at the mainland site and a marginally signif-

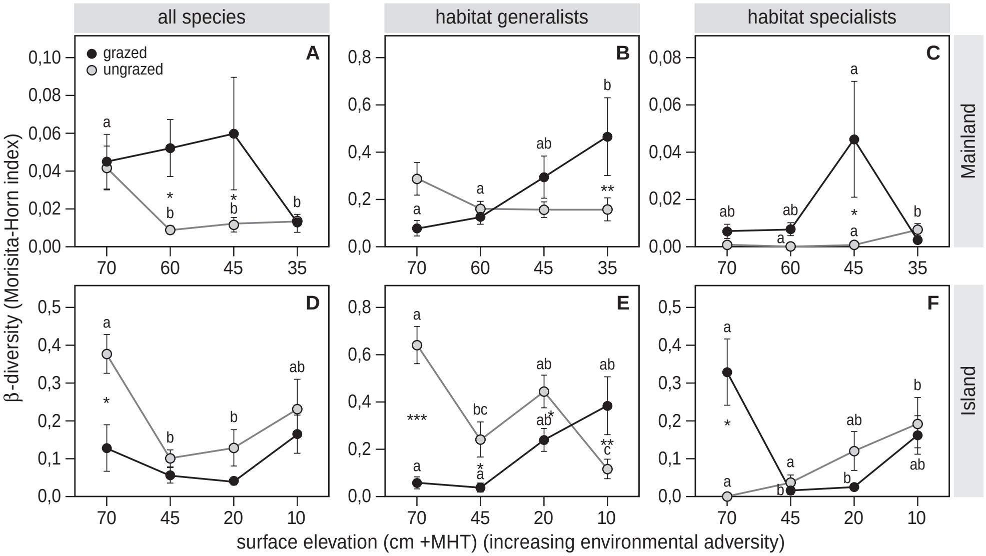

Figure 3.4 Effect of surface elevation on arthropod β-diversity (Morisita-Horn index) on two grazed and ungrazed salt marshes, as calculated between the four traps at each plot. Note difference in scaling of the y-axes. Different letters indicate significant differences between elevational levels, * indicates significant differences between grazing treatments at individual elevational levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Error bars represent standard errors.

Table 3.5 Effects of grazing on overall α- and β-diversity of ground-dwelling arthropods along the entire elevational gradients. Note that at the mainland site, β-diversity is higher under grazing for all groups, whereas at the island site β-diversity is higher in the absence of grazing.

			Mean α- and β-diversity			
			grazed	ungrazed		p
Mainland						
	α-diversity	all species	12.63(±0.3)	14.00 (±0.16)	$\chi^2 = 1.14$	0.29
		habitat generalists	3.88 (±0.07)	4.06 (±0.08)	$\chi^2 = 0.07$	0.79
		habitat specialists	8.75 (±0.27)	9.9 (±0.12)	$\chi^2 = 1.14$	0.27
	β-diversity	all species	0.19(±0.08)	0.03(±0.01)	F = 133.1	<0.001
		habitat generalists	0.47(±0.14)	0.32(±0.08)	F = 25.51	0.001
		habitat specialists	0.014(±0.014)	0.006(±0.004)	F = 11.19	0.002
Island						
	α-diversity	all species	16.00 (±0.20)	14.63 (±0.18)	$\chi^2 = 0.99$	0.32
		habitat generalists	6.19 (±0.13)	4.56 (±0.19)	$\chi^2 = 3.95$	0.047
		habitat specialists	9.81 (±0.20)	10.06 (±0.19)	$\chi^2 = 0.05$	0.82
	β-diversity	all species	0.04(±0.17)	0.48(±0.14)	F = 53.1	0.023
		habitat generalists	0.30(±0.11)	0.62(±0.14)	F = 96.16	<0.001
		habitat specialists	0.28(±0.13)	0.41(±0.17)	F = 12.04	0.001

icant effect at the island site (Table 3.4), which disappeared when doing pairwise comparisons. At the mainland site, β-diversity was generally low (<0.1), indicating similar species compositions of the four traps at each plot. Beta-diversity of habitat generalists increased with decreasing elevation under grazing at both sites (Fig. 3.4B,E), but in the absence of grazing was unaffected at the mainland (Fig. 3.4B), and showed a general decrease at the island site (Fig. 3.4E). Habitat specialist β-diversity increased with decreasing elevation in the absence of grazing at both sites (Fig. 3.4C,F). Under grazing, however, β-diversity showed a peak at intermediate levels at the mainland site (Fig. 3.4C), but a depression at the island site (Fig. 3.4F).

Grazing also had significant effects on overall arthropod β-diversity (Table 3.5). However, for all groups, β-diversity was significantly higher under grazing at the mainland site, but lower at the island site (Table 3.5).

Comparing grazing treatments at the different elevational levels showed varying patterns over the sites and for habitat generalists and specialists (Fig. 3.4). For all species, at the mainland site differences were only significant at the intermediate elevations, (Tukey's test: +60 cm $p = 0.001$; +45 cm $p = 0.01$; Fig. 3.4A), and at the island site only at the highest elevation (Tukey's test: +70 cm $p < 0.001$; Fig. 3.4B). At both sites, β-diversity of habitat generalists was higher under ungrazed conditions at the highest elevations, but lower on the lowest elevations (Fig. 3.4B,E). The habitat specialists showed the opposite pattern, with β-diversity highest under grazing at high elevations, but lowest at low elevations (Fig. 3.4C,F).

DISCUSSION

Elevation and grazing

We hypothesised that an increase in environmental adversity as exhibited on a salt-marsh elevational gradient would decrease both α- and β-diversity of arthropods, and that livestock grazing would impose additional stress on these communities, enhancing the effects of the environmental gradient (Table 3.1). We found support for both hypotheses, but there was considerable variation between sites. The clearest evidence was found for habitat generalists, while the community of habitat specialists showed different, sometimes opposing patterns.

With regard to the complete species pool, we found large differences in species composition along the elevational gradient and between treatments, as is in agreement with previous findings (Irmler et al. 2002, Pétillon et al. 2008). It was, however, surprising to find such limited evidence for a decrease in _-diversity with increasing environmental adversity, as was found on other salt-marsh elevation gradients (Irmler et al. 2002, Finch et al. 2007, Pétillon et al. 2008), but also for other environmental gradients, such as estuarine salinity (Desender and Maelfait 1999) latitude (Willig et al. 2003) and altitude (Rahbek 2005, Nogues-Bravo et al. 2008). Probably, the extent of the gradients at the two sites was too short to exhibit this generally well-established diversity gradient, which can obscure patterns in diversity (McCoy 2002). Without doubt, a decline in species richness of all terrestrial arthropods occurs at the seaward side of the gradient, but because livestock was excluded from this area, and because of the exponential increase in flooding frequency, making pitfall-trapping problematic, we were unable to sample this part of the gradient.

Despite the large differences in community composition between grazed and ungrazed salt marshes, there was no effect of grazing on α-diversity. Previous research has shown varying effects of grazing on arthropod α-diversity. Some researchers found α-diversity of carnivorous arthropods to be higher in ungrazed marshes, which was attributed to an increase in habitat generalists after the establishment of *Elytrigia atherica*, and consequently a proportional decrease of habitat specialists (Andresen et al. 1990, Pétillon et al. 2007). Others did not find a difference in α-diversity between grazed and ungrazed salt marshes (Pétillon et al. 2007, Ford et al. 2013). This may have been caused by differences in stocking density, since the two salt marshes we studied, and the marsh studied by Ford et al. (2013) were grazed at low to moderate stocking densities, while under high stocking densities lower α-diversity is often found (Andresen et al. 1990, Pétillon et al. 2007, van Klink et al. 2013). Grazing at moderate densities therefore seems not to be detrimental to species richness of carnivorous arthropods, though large differences in species composition between grazed and ungrazed marshes are generally found (Andresen et al. 1990, van Klink et al. 2013).

We found a general decline in β-diversity with increasing environmental adversity, as is in agreement with ecological theory (Chase 2007), although the decline was neither linear nor monotonic. Grazing caused opposing differences in β-diversity over the two sites. At the mainland site, β-diversity was higher under grazing, whereas at the island site the opposite was true. At two mainland sites at the German Wadden Sea coast it was shown that cessation of grazing led to a homogenisation of the community along the elevational gradient (Andresen et al. 1990, Meyer et al. 1995), i.e. decreasing β-diversity. This is in agreement with the results from our mainland site, but contrasts with the island site. It is possible that due to the generally larger species pool of natural island marshes, no homogenisation occurs here, but due to a lack of research on grazing of natural salt marshes, the generality of this pattern is unknown.

Habitat specialists and generalists

Habitat specialists and generalists showed strong differences in response to the elevational gradient and grazing. Generalists were less resilient to the adverse conditions at lower elevations and decreased in α-diversity along the inundation gradient, agreeing with earlier field observations (Pétillon et al. 2005, 2008) and experimental evidence (Bethge 1973, Heydemann 1979, Hemminga and Van Soelen 1988, 1992, Bowdish and Stiling 1998, Schile and Mopper 2006). Only at the ungrazed mainland site did we not find a decrease in α-diversity of habitat generalists with increasing stress. This agrees with observations from other mainland salt marshes, where habitat generalists were able to persist at lower elevations after the establishment of the dominant grass *E. atherica* (Andresen et al. 1990, Pétillon et al. 2005). It however, again contrasts with the pattern at our island site, which might again be a general difference between island and mainland marshes, or a site specific effect.

Beta-diversity of habitat generalists was highest under the most benign conditions (ungrazed high marsh) and under the most extreme conditions (grazed low marsh), indicating that samples are most similar under conditions of intermediate adversity. A similar pattern was found for communities of mountain stream invertebrates, where β-diversity was highest under conditions of very low and very high disturbance (Lepori and Malmqvist 2009). The increase in β-diversity under highly adverse conditions can be explained by low α-diversity, observed in both our data and in the mountain stream invertebrates studied by Lepori and Malmqvist (2009). When α-diversity is low, whereas the potential coloniser pool (γ-diversity) remains the same, it will be unpredictable which of the species will be encountered, and hence β-diversity will increase.

Habitat specialist β-diversity peaked under grazing at elevational levels where α-diversity, for unexplained reasons, was low. Under ungrazed conditions, however, β-diversity of habitat specialists was highest at the lowest elevation at both sites, while α-diversity was relatively high, suggesting that for these species the conditions on ungrazed low marshes are not adverse and other processes than abiotic filtering determine species assemblages.

Conclusions

This research shows that under field conditions, several factors can affect patterns of α- and β-diversity along a gradient of environmental adversity. Firstly, grazing increased the environmental stress arthropods are exposed to, consequently altering diversity pattern along the gradient. Secondly, the patterns were neither linear nor monotonic and showed variability between sites. These may have been caused by any of the differences between the sites (Table 3.3), differences in regional species pools, or stochastic processes, and are regularly reported for diversity gradients (e.g. Escobar et al. 2007, Rowe 2009). Replication over a larger number of sites would thus be necessary to arrive at more general conclusions.

Most importantly, we found strong differences in the response of habitat generalist and specialist species to different types of environmental adversity, which obscured some of the diversity patterns along the environmental gradient. While habitat generalists responded to environmental adversity in accordance with the predictions made by Chase (2007, 2010) and the observations by Lepori and Malmqvist (2009), habitat specialists did not. These often showed opposite responses, thriving under conditions that are highly adverse to habitat generalists. These factors can obscure diversity patterns and complicate the study of α- and β-diversity along environmental gradients. Knowledge of the habitat affiliations and life-history traits of the species in the regional species pool will aid disentangling these complications.

ACKNOWLEDGEMENTS

We thank Maarten Schrama for help with the experimental setup, and Julien Pétillon, Peter van Helsingen and Berend Aukema for help with the arthropod identifications. This study was funded by Het Waddenfonds.

Appendix 3.1 List of species caught under the different treatments on the two sites mainland marsh Noord Friesland Buitendijks NFB and the island marsh Schiermonnikoog and an account of their dispersive abilities. Nomenclature follows Vorst (2010), Platnick (2013) (except for *Pardosa purbeckensis*, often described as a subspecies of *P. agrestis*, but by others considered a valid species (Pétillon et al. 2007)) and Aukema & Rieger (1995-2006). Salt-marsh specialists are denoted bold.

	Mainland		**Island**	
species	grazed	ungrazed	grazed	ungrazed
Araneae				
Agyneta decora				1
Allomengea scobigera		17	4	131
Alopecosa pulverulenta			1	14
Arctosa leopardus			2	
Argenna patula	1		18	6
Bathyphantes approximatus		20		
Bathyphantes gracilis	36	8	11	1
Centromerita bicolor		1		
Centromerita concinna		1		
Clubiona stagnatilis	3		2	2
Collinsia inerrans	6			
Diplostyla concolor				9
Drassyllus pusillus			1	1
Enoplognatha mordax	19	3		1
Erigone atra	164	1	213	50
Erigone dentipalpis	25		127	2
Erigone longipalpis	1656	56	1481	63
Gnathonarium dentatum			1	
Gonatium rubens			1	
Hahnia nava			1	4
Hypomma bituberculatum	19	2	11	38
Larinioides cornutus			1	
Leptorhoptrum rubustum	26	193		
Micaria pulicaria				1
Microlinyphia pusilla				1
Oedothorax apicatus				1
Oedothorax fuscus	210	14	670	5
Oedothorax retusus	251	127	203	57
Pachygnatha clercki	118	239	35	128
Pachygnatha degeeri	291		46	29
Pardosa amentata		19		
Pardosa nigriceps				1
Pardosa prativaga				4
Pardosa pullata				1
Pardosa purbeckensis	101	2621	219	476
Pelecopsis paralella	1		12	4
Phlegra fasciata				1
Pirata hygrophilus		1		
Pirata piraticus		12	1	
Pocadicnemis juncea				1
Pocadicnemis pumilla		6	3	
Porhomma pygmaeum			4	
Praestigia duffeyi	1	2	162	555
Robertus arundineti	23	1		2
Robertus lividus		1	1	3
Satilatlas briteni			1	
Silometopus ambiguus			23	
Stemonyphantes lineatus			2	14
Ceratinopsis stativa				1
Tenuiphantes mengei			8	2
Tenuiphantes tenuis	2		12	8
Tiso vagans			1	
Trochosa ruricola	1	36	1	8
Walckenaeria antica				1
Walckenaeria atrotibialis				1

Appendix 3.1 Continued

species	**Mainland** grazed	**Mainland** ungrazed	**Island** grazed	**Island** ungrazed	
Araneae					
Walckenaeria kochi		33		1	
Xysticus cristatus			4	1	
Zelotes electus			1		
Zelotes latreillei				6	
Araneae Total	2954	3414	3284	1636	
Araneae salt-marsh specialists	1778	2682	1903	1101	
Araneae species number	20	23	35	41	
Coleoptera					wing form
Acupalpus elegans	1				macropterous
Amara aenea			3		macropterous
Amara familiaris				2	macropterous
Anisodactylus binotatus	1				macropterous
Bembidion aeneum	484	111		15	wing dimorfic
Bembidion guttula		1			wing dimorfic
Bembidion minimum	51	25	167	253	macropterous
Bembidion normannum	1	4	5	14	macropterous
Bembidion properans			1		wing dimorfic
Bembidion quadrimaculatum				1	macropterous
Bembidion semipunctatum			1		macropterous
Bembidion varium	2	15		1	macropterous
Calathus melanocephalus			8	2	wing dimorfic
Clivina fossor	6	5	1	4	wing dimorfic
Dicheirotrichus gustavii			14	32	macropterous
Dyschirius globusus			31	75	macropterous
Dyschirius salinus			5	5	wing dimorfic
Loricera pilicornis		3	1	3	macropterous
Notiophilus aquaticaus			2		wing dimorfic
Poecilus cupreus		1			macropterous
Pogonus chalceus	5	11	3	6	wing polymorphic
Pogonus luridipennis	6	1			macropterous
Pterostichus melanarius		1			wing polymorphic
Pterostichus niger		4			macropterous*
Pterostichus strenuus				1	wing polymorphic
Harpalus rufipes				1	macropterous
Carabidae Total	557	182	242	415	
Carabidae salt-marsh specialists	549	167	194	326	
Carabidae species number	9	12	13	15	
Heteroptera					
Chiloxanthus pilosus			125	3	macropterous
Halosalda lateralis			2		macropterous
Salda littoralis		24	7	28	wing polymorphic
Saldula palustris			5	1	macropterous
Heteroptera Total	0	24	139	32	
Heteroptera species number	0	1	4	3	
grand total	3511	3620	3665	2083	
grand total species number	29	36	52	59	
salt-marsh specialist individuals	2327	2873	2236	1459	
salt-marsh specialist species	10	10	13	11	

* Winged species, but no functional flight muscles and no flight observations in Western Europe (Turin 2000).

Chapter 4

Grazed vegetation mosaics do not maximize arthropod diversity: evidence from salt marshes

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ABSTRACT

Light to moderate grazing in grasslands can create vegetation mosaics of short grazed vegetation and tall ungrazed vegetation. These mosaics have been proposed to maximize plant and animal species richness, yet experimental evidence, especially regarding arthropods is scarce. This study compares abundance, richness and species composition of arthropods in grazed mosaics to those of homogeneous short and tall vegetation.

We sampled arthropods on three German coastal salt marshes where grazing with three densities (high, moderate and none) was installed in 1989 on previously intensively grazed plots. Stable vegetation mosaics had developed under moderate stocking densities. We collected spiders, beetles, bugs and moth larvae by suction sampling in a stratified random sampling design.

Treatments had caused large differences in plant composition after 20 years, which were reflected in the arthropod community. Most species showed a clear preference for either short or tall vegetation, but some species were most abundant in grazed mosaics. Arthropod richness and composition were similar in patches of short vegetation in moderately and highly stocked plots, while patches of tall vegetation were similar to ungrazed plots. Surprisingly, however, grazed mosaics were not richer in species than homogeneous tall vegetation, despite the co-occurrence of species from short, tall and mosaic vegetation.

We conclude that, although arthropod richness of salt marshes is greatly enhanced when stocking density is decreased, this cannot substitute ungrazed marshes for conservation of arthropod diversity. However, long term cessation leads to the disappearance of several species, and therefore the possibilities of rotational grazing should be explored.

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INTRODUCTION

European coastal salt marshes are productive grasslands subject to frequent flooding by sea water, and are of high nature conservation value because of their species-poor, but highly characteristic plant and arthropod communities. Grazing by large herbivores is often used as a tool in conservation management in salt marshes to maintain plant species richness and to create heterogeneity (Bouchard et al. 2003). While cessation of grazing leads to a dominance of tall grasses, under grazed conditions a more species-rich short vegetation is maintained (Bakker et al. 2003), facilitating small vertebrate herbivores such as geese (Bos et al. 2005). Under moderate to low stocking densities, stable mosaics of short, grazed vegetation and tall ungrazed vegetation develop (Berg et al. 1997, Versteegde 2011). With respect to invertebrates, species richness of beetles, spiders and bugs increases after cessation of grazing, due to an increase in ubiquitous species, while under grazed conditions salt-marsh specialists dominate (Andresen et al. 1990, Pétillon et al. 2007, Ford et al. 2013). Moth communities, on the other hand, respond sensitively to grazing, and are only able to maintain species richness under very low stocking densities (Rickert et al. 2012).

The creation of a mosaic of short and tall vegetation can occur in almost any grassland type (Adler et al. 2001) if large grazers visit certain patches frequently (the so-called grazing lawn), while other patches are only grazed incidentally or remain ungrazed (McNaughton 1984, Adler et al. 2001, Dumont et al. 2012). In several ecosystems these structural vegetation mosaics have been shown to be beneficial for species richness of plants (Olofsson et al. 2008, Marion et al. 2010) but studies of the effects on arthropods are scarce.

In general, high densities of large grazers are detrimental to arthropod species richness, and richness will increase when densities decrease (Morris 2000). At low densities or in ungrazed situations, however, results are inconsistent. Many studies have shown a linear or asymptotic increase of arthropod richness with decreasing grazer density, with richness peaking in the absence of herbivores (Kruess and Tscharntke 2002a, e.g. 2002b, Öckinger et al. 2006). This is usually attributed to decreased disturbance (Kruess and Tscharntke 2002b) or an increase in vertical vegetation complexity (Kruess and Tscharntke 2002a), which is known to be one of the most important factors determining arthropod species richness (Luff 1966, Lawton 1983, Tscharntke and Greiler 1995). Other studies found a positive effect of grazing on arthropod richness (e.g. Joern 2005, Vulliamy et al. 2006), which was attributed to increased vegetation heterogeneity created by large grazers. Most arthropod species show a specific response to grazing, with some species being more abundant in short grazed vegetation, while others are more abundant in tall, ungrazed vegetation (e.g. Dennis et al. 1997, 2001, Woodcock et al. 2007). A mosaic of short and tall vegetation should therefore optimize species richness. Yet, despite the generally positive relation between habitat heterogeneity and animal richness (Tews et al. 2004), evidence supporting this is limited.

For several thermophilous insects, vegetation mosaics consisting of a patchwork of short and tall vegetation have been shown to be essential to complete their life cycles

(Cherrill and Brown 1992, Roy and Thomas 2003). At the community level Joern (2005) found a positive relation between vegetation heterogeneity and grasshopper species richness in prairie grasslands, but other studies did not find such a clear result. In grazed mosaics, patches of tall vegetation were found to be richer in arthropod species and individuals than patches of short vegetation (Cherrett 1964, Dennis et al. 1998, Helden et al. 2010). Furthermore, species richness was negatively related to management intensity, suggesting that vegetation height rather than mosaic structure determines species richness (Dennis et al. 1998). This was supported by Helden et al. (2010) who found that the proportion of arthropods living in patches of tall vegetation decreased when the surrounding vegetation was taller. These studies, however, were conducted in short-term grazing experiments and effects of long term vegetation changes in these mosaics were not yet pronounced. Investigations of the long-term impact of patch grazing on arthropod communities are, therefore, urgently needed. We aim to fill this knowledge gap by comparing mosaics of tall, late successional vegetation and short grazing lawns created by 20 years of experimental grazing to homogeneous tall and short vegetation found under ungrazed conditions and intensive sheep grazing, respectively, in a salt marsh ecosystem.

We hypothesize that most arthropod species will show a clear preference for either short or tall vegetation, but that some species will peak in grazed mosaics (H1). The difference in arthropod communities of grazed and ungrazed salt marshes will be reflected in the species richness, abundance and composition of arthropod communities in structural vegetation mosaics (H2) (i.e. patches of short vegetation will resemble homogeneously short grazed vegetation, and patches of tall vegetation will resemble ungrazed salt marshes). Consequently, because of the co-occurrence of species associated with tall vegetation, short vegetation, and mosaics, grazed mosaics should sustain higher arthropod species richness than homogeneous vegetation (H3).

METHODS

Study sites

This study was performed at three sites on the Wadden Sea coast of Schleswig-Holstein, Northern Germany (see Fig. 1.2). At these sites, experimental sheep grazing with three stocking densities (high: 10 sheep ha^{-1}, moderate: 3-4 sheep ha^{-1} and abandonment: 0 sheep ha^{-1}) has been maintained continuously for over two decades (Stock et al. 2005). The marshes were grazed throughout summer (May – October) and sheep were only removed during flooding events. All sites are man-made salt marshes, originally created for land reclamation using sedimentation fields, but are now part of the protected Wadden Sea National Park and UNESCO world heritage site.

The salt marshes of Friedrichskoog (FK) (54°02`N, 8°54`E, currently ~70cm above mean high tide (MHT)) and Sönke-Nissen-Koog (SNK) (54°38`N, 8°50`E, currently ~40 cm above MHT), have been part of a grazing experiment that started in 1988. At each site, grazing regimes were established on adjacent paddocks that were intensively grazed until 1988 (ca. 10 sheep ha^{-1}), stretching from the sea wall to the intertidal flats. For details on the experimental setup see Dierßen et al. (1994), Meyer et al. (1995). Each treatment level was present once at each site, but experimental units were large (11–15 ha). FK represents a typical higher salt marsh, where the grass *Festuca rubra* is the dominant plant species, while at SNK a typical lower salt marsh is found, dominated by the grass *Puccinellia maritima*. The salt marshes of the Hamburger Hallig (HH) (54°36`N, 8°50`E, currently ~55 cm above MHT) have been under stable grazing management since 1991, and are characterised by plant species of both high and low salt marshes (for details see Stock et al. 2005).

At each site, we investigated three different vegetation patterns that were created by grazing: high stocking densities (10 sheep ha^{-1}) maintained homogeneous short vegetation with many early successional plant species, no grazing (0 sheep ha^{-1}) led to late-successional homogeneous tall vegetation, and grazing at moderate stocking densities (3-4 sheep ha^{-1}) created a mosaic of patches of short and tall vegetation. The patches of tall vegetation were all similar in size (4-10 m^2) and were spaced at least 20 m apart, separated by one or more ditches. They covered maximum 30% of each 4 ha plot area, and had developed a distinctly different vegetation composition from the short grazed vegetation. The three treatments therefore represented four structural vegetation types: homogeneous short vegetation, homogeneous tall vegetation, and short and tall vegetation (referred to as "mosaic short" and "mosaic tall", respectively) at moderate stocking densities.

Sampling design

At each site, a representative elevation above mean high tide (MHT) was chosen as mean plot elevation matching with the dominant plant community, because elevation above MHT strongly influences arthropod community composition in salt marshes (Irmler et al. 2002). In each of the three paddocks per site, we established a plot of 200 m × 200 m. Each plot contained 16 sampling locations, at least 10 m apart and restricted to the mean plot elevation ±10 cm.

In plots with homogeneous vegetation, 16 locations were chosen with the following restrictions: distance between locations was at least 10m, and due to the rigid ditching structure (spaced 10m apart) typical for man-made mainland salt marshes, all sampling locations were separated by at least one ditch. The exact sampling locations were then randomly selected by throwing a stick downwind. In the vegetation mosaics we used a stratified random sampling design, with eight locations in mosaic short vegetation, and eight locations in mosaic tall vegetation. Each sampling location was located in a different patch of tall vegetation. Patches of tall and short vegetation were defined following Bakker et al. (1984): vegetation > 10 cm and with a distinct litter layer was classified as a tall patch, whereas short patches featured short vegetation, mostly < 5 cm, and no litter layer.

Each location was sampled four times in 2010 (May, June, July, September). In June, the sampling at SNK was disturbed by a flood, and this sampling round was therefore omitted from analyses for this site. All measurements of vegetation and samples of arthropods were taken in a circular sampling ring of 30 cm in diameter (1/12 m^2), which we placed on the soil, anchored by two metal pins.

Vegetation measurements

During each visit we recorded vegetation height to the nearest cm inside the sampling ring by lowering a styrofoam drop-disk (diameter 20 cm, weight 45 g) along a calibrated stick onto the vegetation (Stewart et al. 2001). Thereafter we estimated cover percentages of all plant species inside the ring. Plant nomenclature follows Van der Meijden (2005).

Arthropod sampling

We sampled arthropods within the ring-area using a reversed leaf blower (Echo Shred 'n' Vac, diameter 15 cm, maximum air velocity 73 ms^{-1}) that was equipped with a 1mm mesh net. The sampling ring was covered by fine mesh gauze when placed on the vegetation to prevent arthropods from escaping. After an initial 30 seconds of suction sampling we removed the net and took vegetation measurements (see above). Because suction sampling efficiency is known to decrease with increasing vegetation height (Brook et al. 2008), we removed and sieved all above-ground biomass to height of approximately 3 cm from the sampling ring after the first suction round and conducted a second suction-round. All invertebrates caught during suction sampling and biomass removal were collected in the field using manual exhausters and stored in 70% alcohol. The debris of the second suction was collected in plastic bags for further sorting.

We identified all adult individuals of spiders (Araneae), beetles (Coleoptera), true bugs (Heteroptera), plant- and leafhoppers (Auchenorrhyncha) to species level. Moth larvae (Lepidoptera) were identified in the field and were only assessed during the September sampling.

Data analysis

VEGETATION CHARACTERISTICS

We assessed small scale differences in vegetation height and species richness between the four structural vegetation types using generalised linear mixed models (GLMM) (lme4 library (Bates et al., 2012)) with a nested structure of site/stocking density/sample (n = 144). Significance was assessed using quasi-likelihood estimation. Because of heteroscedacity in the variance of vegetation height, data were log-transformed. Plot scale species richness was calculated pooling all 16 samples of each plot (n = 9). Plot scale richness was assessed using Poisson-distributed GLMM's with site as random factor. Post-hoc tests were done using Tukey's HSD from the multcomp library (Hothorn et al. 2008). All statistical analyses were done using R 2.15.2 (R Core Team 2013).

ARTHROPODS

Because of the high conservation interest of salt-marsh specific arthropod species, we performed all analyses on all species combined and on salt-marsh specialists separately. We classified all species restricted to salt influenced habitats (including inland salt pans), salt-marsh specialist according to the following literature: spiders: Hänggi et al. (1995), ground beetles: Turin (2000), other beetles: Koch (1989-1992), true bugs: Wachmann et al. (2003-2008), plant- and leafhoppers: Nickel (2003) and Microlepidoptera: Agassiz (2000).

Species-specific responses were assessed for species with an incidence of ten or more (n = 54). We tested these54 species for differences in sample-based abundance between treatment levels, and recognised four different response types to increasing stocking density: 1) negative response: highest abundance under ungrazed conditions; 2) positive response: highest abundance in densely stocked plots; 3) unimodal response: highest abundance under moderate stocking densities; 4) neutral: no significant differences between stocking densities.

Species that were caught under one stocking density only were directly assigned to the corresponding response type. For all species that were found in more than one treatment level, we fitted linear models. Mixed models with site as random factor were used for species that were present at more than one site. All models were based on Poisson or negative-binomial distributions, where necessary corrected for over-dispersion. We report the number of species following each response type for all species and for salt-marsh specialists.

ARTHROPOD SPECIES RICHNESS AND ABUNDANCE

For statistical analysis, catches from the four sampling rounds per location were pooled. To compare mean (sample-based) species richness and abundance over the different structural vegetation types, we fitted Poisson-distributed linear mixed models with a nested structure of site/stocking density/sample as random factor. To test whether differences in species richness between structural vegetation types were simply caused by differences in abundance (Magurran 2004) we also fitted models using abundance as well as vegetation type as fixed factors and site as random factor. We applied backward model selection on both the random and the fixed parts of all models based on AIC's.

Total (plot based) species richness per plot was calculated pooling all 16 samples of each plot. A Poisson-distributed mixed model was fitted using stocking density as fixed and site as random factor. We fitted both model types for all species combined and for salt-marsh specialists separately. We visualised the overall difference in community composition between structural vegetation types by non-metric multidimensional scaling (NMDS) with Jaccard dissimilarities using the vegan library (Oksanen et al. 2013).

Finally, in order to model the ratio of short and tall vegetation in a grazed mosaic at which arthropod species richness might be optimised, we resampled our data. We divided all 48 samples per site into short or tall vegetation, and took 20 random samples from this pool with 10.000 iterations for different proportions of tall vegetation. The proportion of tall vegetation varied from 100% short vegetation to 100% tall vegetation at 5% intervals. Total richness of the sampled communities was calculated by pooling all samples and we report mean, minimum and maximum values at each proportion for each of our three sites.

RESULTS

Vegetation characteristics

After 20 years of experimental grazing, plant species composition differed strongly between short and tall vegetation, both between the ungrazed and the intensively grazed plots and within the grazed mosaics (Table 4.1). Short vegetation was still dominated by grazing tolerant grasses such as *Puccinellia maritima* at SNK and *Festuca rubra* at FK and HH, and several short-statured forbs. In the ungrazed, homogeneous tall vegetation large cover percentages were reached by the tall, late successional grass *Elytrigia atherica* and the dwarf shrub *Atriplex portulacoides*, while short-statured forbs such as *Glaux maritima* and *Plantago maritima* had disappeared. Patches of tall vegetation in the grazed mosaics differed somewhat from the homogeneous tall vegetation, with species such as *Artemisia maritima* and *Juncus gerardii* reaching high cover percentages (Table 4.1).

Mean vegetation height of both short vegetation types was around 5 cm, whereas both tall vegetation types were significantly taller, around 20 cm in height ($\chi^2 = 145.9$, $p < 0.001$, Table 4.1). At the small scale, mean plant species richness was highest in the short vegetation types and lowest in the homogeneous tall vegetation ($\chi^2 = 12.8$, $p = 0.005$, Table 4.1). Richness of the mosaic short and mosaic tall vegetation did not differ significantly (Table 4.1). Plant species richness at plot scale did not differ between any of the treatment levels ($\chi^2 = 1.87$, $p = 0.39$), although richness was lowest in the ungrazed plots at all sites (mean over three sites: homogeneous tall: 10.33, mosaic: 13.33, homogeneous short: 14).

Arthropods

In total 3,766 individuals of 154 arthropod species were caught. Spiders were represented by 53 species, beetles by 68 species, true bugs by 12, plant- and leafhoppers by 12 and moth larvae by 9 species of which *Eucosma tripoliana* and *E. rubescana* are indistinguishable during the larval stages (Rickert 2011). Species richness was lowest at our lowest elevated site, SNK, with 65 species and highest at our highest elevated site, FK, with 112 species.

Species-specific responses

We found 54 species with an abundance >10, of which 22 were salt-marsh specialists. . About 50% of the species showed a negative response to grazing, both for salt-marsh specialists and all species combined, whereas around 20% responded positively (Fig. 4.1). Only six species (11%) had highest abundances in grazed mosaics (Fig. 4.1). Three of these species are herbivorous species living only on the halophytic plant species *Artemisia maritima* (Coleophora a*rtemisiella (Lepidoptera*: Coleophoridae) and *Europiella decolor* (Heteroptera: Miridae)) and *Juncus gerardii* (*Coleophora adjunctella* (Lepidoptera: Coleophoridae)). They responded to the increased cover of their host plants (Pearson correlation: *C. artemisiella*: r = 0.81; *E. decolor*: r = 0.77; *C. adjunctella*: r = 0.55, Table 4.2). The other three species are small spiders that are associated with a wide variety of grassland habitats (*Pachygnatha degeeri* (Tetragnathidae), *Troxochrus scabriculus* and *Oedothorax retusus* (Linyphiidae) (Hänggi et al. 1995, Harvey et al. 2002) (see Appendix 4.1). Grazed mosaics

Table 4.1 Characteristics of plant communities over four structural vegetation types at three salt marshes in the German Wadden Sea after 20 years of experimental grazing. Structural vegetation types were created by sheep grazing, where high stocking densities (10 sheep ha^{-1}) led to homogeneous short vegetation, moderate densities (3-4 sheep ha^{-1}) led to a mosaic of short and tall vegetation and no grazing (0 sheep ha^{-1}) led to homogeneous tall vegetation. Letters denote significant differences according to Tukey tests ($p < 0.05$). The three species with the highest cover percentage pooled over four sampling dates were considered dominant.

	Homogeneous short	**Structural mosaic (4 sheep ha^{-1})**		**Homogeneous tall**
	(10 sheep ha^{-1})	Mosaic short	Mosaic tall	(0 sheep ha^{-1})
Mean no species/0.33m^{2} (±se)	7.3 (±0.23)^{a}	5.8 (±0.33)^{ab}	5.3 (±0.31)^{bc}	4.1 (±0.22)^{c}
Mean canopy height (±se)	5.0 (±0.24) cm^{a}	5.8 (±0.49) cm^{a}	19.4 (±1.26) cm^{b}	24.5 (±1.27) cm^{c}
Dominant species (total%cover)				
Friedrichskoog	*Festuca rubra* (35%)	*F. rubra* (49%)	*Elytrigia atherica* (46%)	*F. rubra* (56%)
	Agrostis stolonifera (32%)	*A. stolonifera* (43%)	*F. rubra* (27%)	*E. atherica* (33%)
	Armeria maritima (12%)	*Glaux maritima* (4%)	*Juncus gerardii* (21%)	*A. stolonifera* (10%)
Hamburger Hallig	*Puccinellia maritima* (35%)	*F. rubra* (55%)	*F. rubra* (52%)	*E. atherica* (46%)
	F. rubra (35%)	*G. maritima* (19%)	*Artemisia maritima* (30%)	*F. rubra* (36%)
	G. maritima (8%)	*Arm. maritima* (10%)	*J. gerardii* (8%)	*Art. maritima* (6%)
Sönke-Nissen Koog	*P. maritima* (49%)	P. *maritima* (51%)	*F. rubra* (50%)	*P. maritima* (27%)
	F. rubra (27%)	*F. rubra* (22%)	*Atriplex portulacoides* (17%)	*A. portulacoides* (23%)
	Salicornia spp (7%)	*Aster tripolium* (12%)	*E. atherica* (17%)	A. *tripolium* (20%)

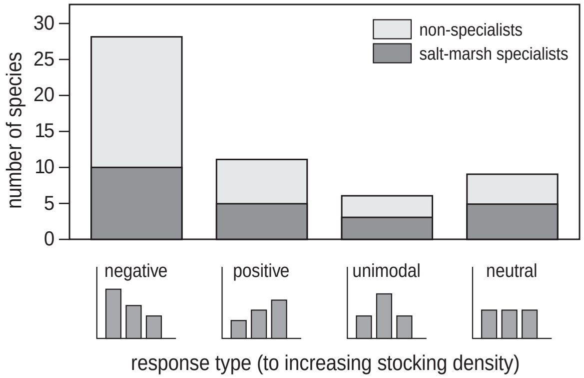

Figure 4.1 Number of arthropod species (total abundance >10) representing each of four response types to increasing stocking densities (no grazing, 3-4 sheep ha^{-1}, and 10 sheep ha^{-1}) on three salt marshes in the German Wadden Sea. Bars are subdivided in salt-marsh specialists and non-specialists (mostly ubiquitous and common species). All species, their habitat classification and response type are listed in Appendix 4.1.

Table 4.2 Pearson correlation coefficients of abundance of monophagous herbivores and cover percentage of their host plants over all treatments combined. Correlation coefficients were only calculated for insect species with an abundance >9. Sites where the herbivore was absent were not considered in the analysis. Stars denote significance levels: *: p < 0.05; **: p < 0.01; ***: p < 0.001

	Aster tripolium	*Artemisia maritima*	*Atriplex littoralis*	*Atriplex portulacoides*	*Glaux maritima*	*Juncus gerardii*	*Plantago maritima*	Grasses: *Puccinellia maritima* and *Festuca rubra*
Eucosma tripoliana, and *Eucosma rubescana* (Lepidopera: Tortricidae)***	0.35							
Europiella decolor (Heteroptera: Miridae)***		0.77						
Eucosma lacteana (Lepidoptera: Tortricidae)***		0.41						
C*oleophora artemisiella* (Lepidoptera: Coleophoridae)***		0.81						
Scrobipalpa nitentella (Lepidoptera: Gelichidae)**			0.44					
Coleophora atriplicis (Lepidoptera: Coleophoridae)				0.06				
P*elenomus zumpti* (Coleoptera: Curculionidae)*					0.25			
Coleophora adjunctella (Lepidoptera: Coleophoridae)***						0.55		
Trichosirocalus thalhammeri (Coleoptera: Curculionidae)*							0.29	
W*hittleia retiella* (Lepidoptera: Psychidae)								0.15
Anoscopus limicola (Auchenorrhyncha: Cicadellidae)								-0.06
Aphrodes aestuarina (Auchenorryncha: Cicadellidae)								0.03
Psammotettix putoni (Auchenorryncha: Cicadellidae)*								0.21

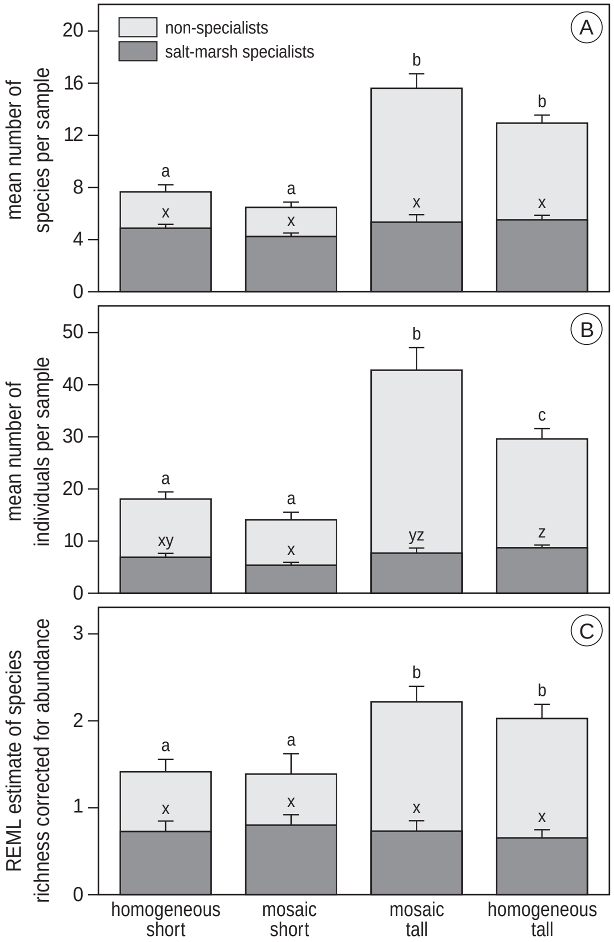

Figure 4.2 Mean arthropod species richness (A), abundance (B) and richness corrected for abundance (C) per sample (n = 144) of salt-marsh specialists and non- specialists over four different structural vegetation types. Arthropods were sampled four times over the summer of 2010 on ø 30cm samples. Different letters for all species combined (a-c) and for salt-marsh specialists (x-z) denote significant differences ($p < 0.05$).

supported considerable numbers of individuals of every response type. Averaged over all three sites, 41% of the individuals present in the grazed mosaics belonged species with a negative response type, 19% of a positive response type, and 29% of the unimodal response type. This is in stark contrast to the homogeneous tall, ungrazed vegetation, where 82% of the individuals belonged to species with a negative response to grazing, and the homogeneous short vegetation, where 69% belonged to species with a positive response type. Species not showing a significant response (neutral response type) were present under all stocking densities, representing about 10% of individuals.

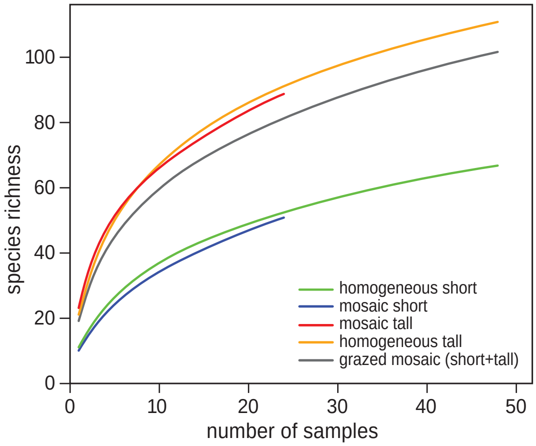

Figure 4.3 Sample based species accumulation curves of all treatments and structural vegetation types (Grazed mosaic = mosaic short + mosaic tall), combined over the three sites, showing the almost identical relation of species and samples in tall vegetation types (homogeneous tall and mosaic tall) and the short vegetation types (homogeneous short and mosaic short).

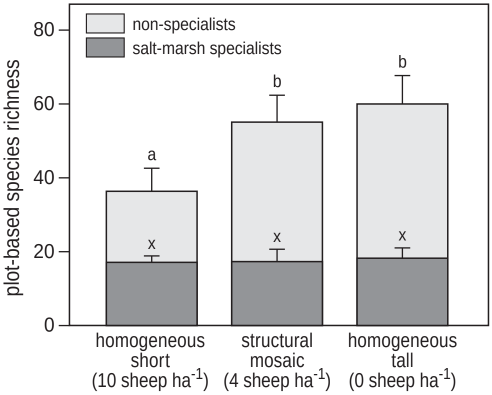

Figure 4.4 Mean plot-based species richness of arthropods, pooled over 16 samples per treatment per site (n = 9), under three different stocking densities. Different letters denote significant differences (all species combined a-b, salt-marsh specialists x-y) according to Poisson distributed GLMM's.

Species richness and community composition

Mean arthropod species richness and abundance per sample more than twice as high in tall vegetation types as in short vegetation, and highest in mosaic tall vegetation (richness: $\chi^2 = 80.2$, $p < 0.001$; abundance: $\chi^2 = 63.7$, $p < 0.001$; Fig. 4.2A, 4.2B). Species richness followed a pattern highly similar to abundance, suggesting that differences in species richness might simply be caused by differences in the number of individuals. Yet, incorporating abundance and the abundance*structural type interaction in the model showed that tall vegetation types were indeed richer than short vegetation types ($\chi^2 = 235.6$, $p = 0.001$;

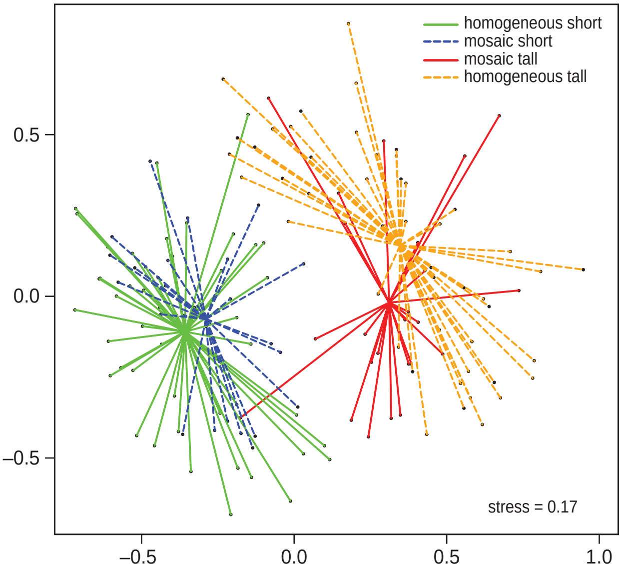

Figure 4.5 Biplot of non-metric multidimensional scaling of arthropod communities from four different structural vegetation types: homogeneous short vegetation (green) under high stocking densities (10 sheep ha^{-1}), short (blue) and tall (red) vegetation in a structural mosaic created under moderate stocking densities (4 sheep ha^{-1}), and homogeneous tall vegetation (orange), 20 years after cessation of grazing. NMDS was performed using Jaccard dissimilarities.

Fig. 4.2C). Abundance and the interaction between abundance and structural vegetation type were highly significant factors explaining species richness, as well. This was supported by sample based species accumulation curves, where curves from the tall vegetation types were almost identical and curves from the short vegetation types very similar to each other (Fig. 4.3). Species richness of salt marsh specialists did not differ between structural vegetation types ($\chi^2 = 5.4$, $p = 0.14$) (Fig. 4.2A), while abundances differed somewhat ($\chi^2 = 15.5$, $p < 0.001$), with slightly more habitat specialists in the ungrazed vegetation (Fig. 4.2B). Higher species richness and abundance in tall vegetation can therefore be fully attributed to the increased occurrence of ubiquitous species. When correcting species richness of salt-marsh specialists for abundance, structural vegetation type was non-significant, and richness of salt-marsh specialists over different vegetation types was fully explained by their abundance ($\chi^2 = 117.34$, $p < 0.001$; Fig. 4.2C).

Pooled (plot-based) species richness of all samples in each plot was significantly lower in homogeneous short vegetation than in mosaics and homogeneous tall vegetation ($\chi^2 = 20.6$, $p < 0.001$; Fig. 4.4), but there was no significant difference between the latter two (Fig. 4.4). As at sample scale, salt-marsh specialists showed no difference in species richness between treatment levels at the plot scale ($\chi^2 = 0.16$, $p = 0.92$; Fig. 4.4). Of the species found in homogeneous short vegetation, 80% were also found in grazed mosaics, whereas only 55% of the species occurring in homogeneous tall vegetation were found in grazed mosaics.

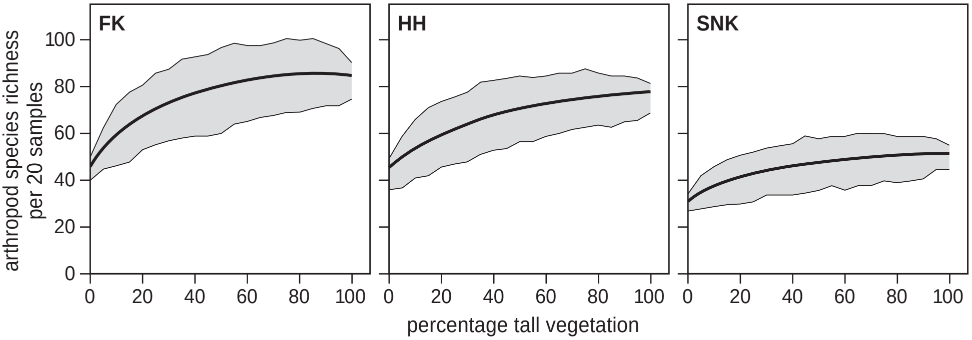

Figure 4.6 Mean, minimum and maximum species richness of re-sampled arthropod communities under increasing proportions of tall vegetation at FK, HH and SNK. Twenty samples were randomly drawn from the pool of 48 samples (representing short vegetation and tall vegetation equally) with 10.000 iterations for each proportion of tall vegetation.

Non-metric multidimensional scaling revealed differences in species composition of short and tall vegetation (Fig. 4.5). The two short vegetation types and the two tall vegetation types formed distinct clusters, but the two vegetation types of the structural mosaic were aligned between the homogeneous short and homogeneous tall vegetation.

Resampling of our arthropod communities showed that the relation between proportion of tall vegetation and arthropod species richness is asymptotic rather than unimodal (Fig. 4.6). Only at FK there is a slight hint of an optimum at around 80–90% tall vegetation.

DISCUSSION

We found strong evidence for H1, that most analysed species showed a clear response to grazing management, and for H2, that the patches of short and tall vegetation in the grazed mosaics function similarly to intensively grazed and ungrazed salt marshes with respect to arthropod abundance, richness and community composition. However, although the grazed mosaics harboured species characteristic of short vegetation, tall vegetation as well as several species that reached peak abundances in grazed mosaics, they were not richer in species than homogeneous tall vegetation, contradicting H3.

Species specific responses

The majority (83%) of the analysed species showed a clear response to grazing management, reaching peak abundances in one of the three treatment levels (Fig. 4.1). This is in contrast to lower numbers of significant reactions reported for similar species groups by other workers (e.g. Dennis et al. (1997, 2001): 17% and Woodcock et al. (2007): 57%). The large proportion of significant responses we found can probably be attributed to the long-term changes in plant and arthropod communities, and the profound difference between the stocking densities.

After 20 years, the ungrazed salt marshes were dominated by tall vegetation, most notably the mat-forming grasses *E. atherica* and *F. rubra* on the two higher elevated sites (FK and HH) and the dwarf shrub *A. portulacoides* at the lower site (SNK). This is a well-known process (e.g. Bakker et al., 2003), causing concern for the conservation of short statured forbs and their associated fauna. Indeed we found that several species of plants and arthropods had been lost from the ungrazed plots, which had been present two years after the start of the experimental grazing at two of our sites (FK and SNK: Meyer et al. 1995, Meyer and Reinke 1996). Among the species that disappeared were several monophagous herbivores of short statured host plants (e.g. *G. maritima* and *Plantago maritima*), but also some carnivorous ground beetles and spiders. Nevertheless, the ungrazed marshes were still most species rich, which can mostly be attributed to an increase of non-habitat specialists. These species are apparently better able to survive the habitat characteristic flooding and salt stress in tall vegetation than in the exposed grazed marsh (Andresen et al. 1990, Meyer et al. 1995, Pétillon et al. 2005, Ford et al. 2013). But also to a number of salt marsh specialists reached peak abundances under ungrazed conditions. This was most obvious for the herbivorous fauna of palatable (e.g. *A. tripolium*) and trampling sensitive (e.g. *Atriplex littoralis*) plant species, as was previously shown by Rickert (2011) for Microlepidoptera during a three year investigation at one of our sites (HH). Although these plants did not reach high cover percentages, they harboured a rich community of herbivorous insects.

In the grazed mosaics, successional changes in the patches of tall vegetation were profound, benefitting several species of halophytes and their associated fauna. Other species, such as the common grassland spiders *O. retusus* and *P. degeeri* reached highest abundances here, whereas being non-responsive to sward management in other ecosystems (Dennis et al. 2001, Woodcock et al. 2007).

In general, our species specific responses curves agree with previous work using pitfall traps (Pétillon et al. 2005, 2007, Ford et al. 2013), comparing grazed and ungrazed marshes, and photo eclectors (Meyer and Reinke 1996, Rickert 2011) over several grazing intensities. Only the typical halophilic ground beetle *Dicheirotrichus gustavii* deviated from previous work. This species has been caught more under grazing using pitfall traps (Ford et al. 2013, van Klink & Schrama unpublished data), but using suction sampling we found this species more abundantly in ungrazed situations, as is in accordance with Meyer and Reinke (1996). Probably this nocturnal species is able to hide in ditch banks or soil crevices under grazing, whereas in the absence of grazing it hides in the thick layer of dead biomass, which we were able to sample after removing all biomass.

Suction sampling is known to be most efficient for sampling canopy dwelling arthropods and is known to be biased towards smaller species (Mommertz et al. 1996, Brook et al. 2008). By removing all biomass, we were able to also sample the litter layer. Nevertheless, we probably under-sampled several species of nocturnal and soil dwelling beetle species, such as the above mentioned ground beetle *D. gustavii* and other typical salt-marsh dwelling beetles (e.g. see Irmler and Heydemann 1986, Meyer and Reinke 1996). But for other beetles and spiders we reached results at least qualitatively comparable to previous studies done using other methods (Irmler and Heydemann 1986, Pétillon et al. 2007, Rickert 2011), supporting the validity of this method.

Species richness and composition

Our results support the importance of tall complex vegetation for maintenance of arthropod species richness that is well known from other ecosystems (Duffey 1962, Luff 1966, Lawton 1983), but also the need for grazed grasslands to maintain short-statured host plants (e.g. Thomas et al. 1986). Surprisingly, though, we did not find highest total species richness in grazed mosaics and also resampling our data did not reveal a definite optimum for arthropod species richness at any proportion of short and tall vegetation. The high similarity of results over our three sites and the consistency of the species specific responses suggest that this may be a general pattern, at least in this ecosystem. However, our sampling was limited to one year and arthropod communities are known to respond strongly to climatic differences (Strong et al. 1984) with some species occurring under specific conditions only. While sampling over more years would have been preferable, consistent results over three different elevational levels (low, mid and high marsh) and the consistent species specific responses might compensate to some extent for possible climatic effects.

A potential explanation for not finding highest arthropod richness in grazed mosaics may be that arthropod richness is limited by one or more external factors. For instance, patch size and isolation may inhibit rare species from reaching viable population sizes or disturbance by large grazers may still be too high for some species, even in patches of tall vegetation. It has been suggested (Hobbs and Swift 1988), and recently shown (Dumont et al. 2012) that stable vegetation mosaics are more likely to develop in productive ecosystems, such as the presented sites, because regrowth of high quality forage is sufficiently fast to provide a continuous food source. This also implies high re-visitation rates of large grazers to foraging patches, increasing trampling, incidental predation and direct resource competition for arthropods.

Properties of grazed mosaics may have large effects on arthropod species richness. Grain size and proportion of tall and short vegetation may differ under different stocking densities (Berg et al. 1997), productivity (Dumont et al. 2012) or grazing history (Versteegde 2011). Dennis et al. (1998) addressed the question how this could affect arthropod communities, but found an asymptotic rather than a unimodal relationship between grain size of the mosaic and arthropod richness, indicating that vegetation height was the determining factor rather than grain size, which is supported by our results. A similar result was found in desert landscapes (Whitehouse et al. 2002), where patchy vegetation patterns occur without intervention of large grazers. Spiders were found to occur either in shrubby patches or bare soil crusts, but overall diversity did not respond to different grain sizes of patchiness (measured as fractal dimension of the patch pattern; (Whitehouse et al. 2002)).

Possibly, arthropod body size plays a role in determining the effect of vegetation heterogeneity on species richness. Studies reporting a positive effect of vegetation mosaics on arthropod species (Cherrill and Brown 1992, Roy and Thomas 2003) or communities (Joern

2005), focussed on large, mobile and thermophilous species, such as grasshoppers, whereas studies that did not find a positive effect (Dennis et al. 1998, this study) considered small, often sedentary species. This supports evidence by Cole et al. (2010) that habitat selection by small, often sedentary species occurs at a different scale than by large, mobile species. For small and sedentary species, grazed mosaics may function as a patchwork of suitable and hostile habitats, following island biogeographical principles (MacArthur and Wilson 1967), where patch size and isolation determine diversity and maximum population size. In contrast, large species may exploit grazed mosaics as large heterogeneous habitats, with different resources (food plants, shelter) and conditions (microclimate) found at close proximity in short and tall vegetation. Therefore, large arthropod species may benefit from vegetation mosaics, whereas small arthropods may not. This may be especially true for thermophilous species, which may exploit vegetation mosaics for thermoregulation. The choice of species and taxonomic groups may thus affect the outcome of studies on species diversity in grazed mosaics.

Conclusion

Our results show the importance of ungrazed salt marshes for the conservation of many arthropod species, even when plant species richness was decreased. Vegetation mosaics created by patch grazing cannot substitute large ungrazed salt marshes, similar to results found by Dennis et al. (1997, 2001) in Scottish upland pastures. Instead, their conservation value mostly lies in the plant species that thrive under moderate stocking densities. However, we also showed that after 20 years of abandonment, several plant and arthropod species disappeared, even though they clearly benefitted from the cessation of grazing at the early stages of the experiment (Meyer and Reinke 1996). In salt marshes as well as other grassland ecosystems, the proliferation of both short and tall statured host plants and their associated fauna occurs shortly after abandonment (Morris, 1967; Meyer et al., 1995). This implies that rotational grazing management might be a valuable option for the conservation of salt marshes and other productive ecosystems, as was shown for calcareous grasslands (Morris et al. 2005) and upland pastures (Farruggia et al. 2012). Finally our results stress the importance of long-term changes caused by the manipulation of stocking density, and the importance of considering spatial heterogeneity when evaluating effects of grazing on arthropods.

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Appendix 4.1 Complete species list of all species collected in 2010 (May, June, July, September) in the salt marshes of Friedrichskoog, Hamburger Hallig and Sönke-Nissen-Koog. Response type to increasing grazing intensity is given for 54 species with an incidence of ten or higher. Salt marsh specialists (according to Hänggi et al. (1995), Turin (2000), Koch (1989-1995), Wachmann et al. (2003–2008), Nickel (2003) and Rickert (2011)) are denoted in bold.

	Response to increasing stocking density	Friedrichs-koog	Ham-burger Hallig	Sönke-Nissen Koog
Araneae				
Agyneta decora (O.P.-Cambridge, 1871)		6		
Agyneta olivacea (Emerton, 1882)		1		
Allomengea scobigera (Grube, 1859)	negative	13	31	9
Alopecosa cuneata (Clerck, 1757)		1		
Alopecosa pulverulenta (Clerck, 1757)		2		
Argenna patula (Simon, 1874)	negative	23	8	1
Praestigia duffeyi Millidge, 1954	negative		29	9
Bathyphantes gracilis (Blackwall, 1841)		6	1	
Centromeria bicolor (Blackwall, 1833)	negative	87	5	3
Styloctetor stativus (Simon, 1881)		1	4	
Clubiona diversa O.P.-Cambridge, 1862		2	0	
Clubiona neglecta O.P.-Cambridge, 1862		7		
Clubiona stagnatilis Kulczynski, 1897	negative	11	15	9
Collinsia inerrans (O.P.-Cambridge, 1885)			1	
Dicymbium nigrum Locket, 1962		1		
Diplostyla concolor (Wider, 1834)	negative	12	3	1
Dismodicus bifrons (Blackwall, 1841)		1		
Enoplognatha thoracica (Hahn, 1833)		5		
Enoplognatha mordax (Thorell, 1875)		1	3	
Erigone arctica (White, 1852)		5	4	
Erigone atra Blackwall, 1833	positive	16	4	
Erigone dentipalpis (Wider, 1834)		5		
Erigone longipalpis (Sundevall, 1830)	positive	6	91	117
Gongylidiellum vivum (O.P.-Cambridge, 1875)		3		
Hahnia nava (Blackwall, 1841)	negative	61		
Hypomma bituberculatum (Wider, 1834)	negative	1	11	
Leptorhoptrum rubustum (Westring, 1851)		2		
Micaria pulicaria (Sundevall, 1831)		3	2	
Micrargus apertus (O. P.-Cambridge, 1870)			1	
Oedothorax fuscus (Blackwall, 1834)	positive	26	18	2
Oedothorax retusus (Westring, 1851)	unimodal	116	126	6
Ozyptila simplex (O.P.-Cambridge, 1862)			1	
Pachygnatha clercki Sundevall, 1823	negative	13	38	21
Pachygnatha degeeri Sundevall, 1830	unimodal	52	5	
Pardosa pullata (Clerck, 1757)		1		
Pardosa purbeckensis F.O.P.-Cambridge, 1895	negative	93	82	26
Pirata piraticus (Clerck, 1757)		1		
Pocadicnemis juncea Locket & Millidge, 1953	negative	52	23	5
Pocadicnemis pumila (Blackwall, 1841)	neutral	10	11	2
Robertus lividus (Blackwall, 1836)		7		
Silometopus ambiguus (O. P.-Cambridge, 1905)		2	3	1
Silometopus reussi (Thorell, 1871)		2	6	
Stemonyphantes lineatus (Linnaeus, 1758)		4	3	
Tenuiphantes tenuis (Blackwall, 1852)		2		
Thanatus striatus C.L. Koch, 1845		2		
Tiso vagans (Blackwall, 1834)	negative	16		1
Trochosa ruricola (De Geer, 1778)	negative	13	3	2
Troxochrus scabriculus (Westring, 1851)	unimodal	50		
Walckenaeria atrotibialis (O.P.-Cambridge, 1878)		1		
Walckenaeria kochi (O.P.-Cambridge, 1872)	negative	13	1	5
Walckenaria vigilax (Blackwall, 1853)			2	
Xysticus cristatus (Clerck, 1757)		4	3	

Appendix 4.1 Continued.

	Response to increasing stocking density	Friedrichs-koog	Ham-burger Hallig	Sönke-Nissen Koog
Coleoptera				
Agriotes lineatus (linnaeus, 1767)	negative	47	34	
Aloconota gregaria (Erichson, 1839)			1	
Amischa analis (Gravenhorst, 1802)		4		
Amischa decipiens (Sharp, 1869)		4		
Acrotona amplicollis (Mulsant & Rey, 1873)		5	1	
Acrotona fungi (Gravenhorst, 1806)		1		6
Atheta vestita (Gravenhorst, 1806)			2	1
Atomaria rhenana Kraatz, 1853		4	2	1
Bembidion aeneum Germar, 1824	neutral		6	11
Bembidion minimum (Fabricius, 1792)	positive	71	26	22
Bembidion normannum Dejean, 1831	neutral	11	5	6
Bembidion obtusum Audinet-Serville, 1821		1		
Bledius tricornis (Herbst, 1784)		2		
Brundinia marina (Mulsant & Rey, 1853)	neutral	10	3	1
Calathus melanocephalus (Linnaeus, 1758)		1		
Cantharis fusca Linnaeus, 1758		1		
Cantharis lateralis Linnaeus, 1758				1
Cantharis rufa Linnaeus, 1758	negative	5	5	
Cassida vittata Villers, 1789	neutral	22	10	8
Chaetocnema hortensis (Geoffroy, 1785)		1		
Chrysolina haemoptera (Linnaeus, 1758)	positive	11		1
Chrysolina staphylaea (Linnaeus, 1758)	negative		26	
Coccidula rufa (Herbst, 1783)			1	
Coccinella septempunctata Linnaeus, 1758	negative	8	4	2
Coccinella undecimpunctata Linnaeus, 1758	positive	31	1	
Dicheirotrichus gustavii Crotch, 1871	negative	1	12	12
Drusilla canaliculata (Fabricius, 1787)		6	3	
Dyschirius globosus (Herbst, 1784)	negative	38	59	2
Dyschirius salinus Schaum, 1843		1	1	
Halobrecta flavipes Thompson, 1861			2	
Helophorus brevipalpis Bedel, 1881	positive	30	38	15
Heterocerus flexuosus Stephens, 1828		1	3	2
Heterocerus maritimus Guérin-Méneville, 1844		1	1	
Lesteva longoelytrata (Goeze, 1777)				1
Limnobaris dolorosa (Goeze, 1777)			1	
Longitarsus plantagomaritimus Dollman, 1912			1	
Longitarsus reichei (Allard, 1860)		1		
Mecinus collaris Germar, 1821		1		
Meligethes aeneus (Fabricius, 1775)	neutral	1	3	17
Nephus redtenbacheri (Mulsant, 1846)		2	6	1
Ochthebius auriculatus Rey,1886	neutral	2	94	70
Tasqius ater (Gravenhorst, 1802)			1	
Otiorhynchus ligneus (Olivier, 1807)	neutral	7	5	
Oxypoda brachyptera (Stephens, 1832)		4		
Pelenomus zumpti (Wagner, 1939)	positive	6	15	6
Philonthus cognatus Stephens, 1832			4	
Philonthus varians (Paykull, 1789)			1	
Phyllobius vespertinus (Fabricius, 1793)	negative	21	27	23
Pogonus chalceus (Marsham, 1802)				1
Polydrusus pulchellus Stephens, 1831		3	3	3
Protapion fulvipes (Geoffroy, 1785)		1		
Psylliodes chrysocephala (Linnaeus, 1758)				1
Ptenidium fuscicorne Erichson, 1845	negative	8	2	
Pterostichus macer (Marsham, 1802)			1	
Quedius simplicifrons Fairmaire, 1862		2		
Rhagonycha fulva (Scopoli, 1763)		5		

Appendix 4.1 Continued.

	Response to increasing stocking density	Friedrichs-koog	Ham-burger Hallig	Sönke-Nissen Koog
Coleoptera				
Sitona lepidus Gyllenhal, 1834		1		
Stenus brunnipes Stephens, 1833		1		
Stenus clavicornis (Scopoli, 1763)		1		
Stenus lustrator Erichson, 1839		1		
Tachyporus dispar (Paykull, 1789)		1		1
Tachyporus hypnorum (Fabricius, 1775)		4	1	2
Tachyporus pusillus Gravenhorst, 1806		4		
Trechus obtusus Erichson, 1837		1		
Trichosirocalus thalhammeri (Schulze, 1906)	positive	10		
Tytthaspis sedecimpunctata (Linnaeus, 1760)		1		2
Xantholinus dvoraki Coiffait, 1956		5	4	
Xantholinus longiventris Heer, 1839			1	
Heteroptera				
Chiloxanthus pilosus (Fallén, 1807)			1	1
Conostethus griseus Douglas and Scott, 1870			1	3
Derephysia foliacea (Fallén, 1807)			2	
Drymus ryeii Douglas & Scott, 1865		1		
Europiella decolor (Uhler, 1893)	unimodal		40	7
Fieberocapsus flaveolus (Reuter, 1871)			1	
Leptoterna ferrugata (Fallén 1807)		1		1
Nabis flavomarginatus Scholtz, 1847			2	2
Orthotylus moncreaffi (Douglas and Scott, 1874)			2	5
Salda littoralis (Linnaeus, 1758)				2
Saldula palustris (Douglas, 1874)			1	8
Trigonotylus ruficornis (Geoffroy in Fourcroy, 1785)		2		3
Auchenorrhyncha				
Anoscopus limicola (Edwards, 1908)	negative	1	56	179
Aphrodes eastuarina (Edwards, 1908)	negative		42	58
Conosanus obsoletus (Kirschbaum, 1858)			1	3
Deltocephalus pulicaris (Fallén, 1806)		1		
Euscelis incisus (Kirschbaum, 1858)			3	
Javesella pelucida (Fabricius, 1794)			1	
Neophilaenus lineatus (Linnaeus, 1758)			1	
Philaenus spumarius (Linnaeus, 1758)			1	
Psammotettix putoni (Then, 1898)	positive	50	54	148
Streptanus aemulans (Kirschbaum, 1868)	negative	1	22	52
Streptanus sordidus (Zetterstedt, 1828)		3	5	1
Xanthodelphax straminea (Stal, 1858)		1		
Lepidoptera				
Coleophora adjunctella Hodgkinson, 1882	unimodal		10	
Coleophora artemisiella Scott, 1861	unimodal		153	6
Coleophora asteris Mühlig, 1864				1
Coleophora atriplicis Meyrick, 1928	neutral	13	10	12
Eucosma lacteana (Treitschke, 1835)	negative		10	4
Eucosma tripoliana (Baret, 1880) / ***E. rubescana*** (Constant, 1895)	negative		59	63
Scrobipalpa nitentella (Fuchs, 1902)	negative	34		
Scrobipalpa salinella (Zeller, 1847)		1		
Whittleia retiella (Newman, 1847)	negative	29	20	
Total number of species		112	95	65
Total number of individuals		1315	1452	999

Chapter 5

Defoliation and soil compaction jointly drive grazing effects on plants and soil arthropods on fine-textured soil

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ABSTRACT

Large herbivores exert major impacts on plant and arthropod communities through defoliation, defecation and trampling. Although the first two processes have been intensively studied, recent work stresses the importance of herbivore trampling and the associated soil compaction on composition of above- and belowground communities, especially on wet, fine-textured soils. Soil compaction reduces habitable pore space and soil aeration, with poorly known consequences for both plant and animal communities. On a clay-rich salt marsh at the Dutch Wadden Sea coast, we established a full-factorial manipulation experiment, aiming to disentangle the relative importance of defoliation and soil compaction on plant and arthropod communities.

In a previously ungrazed salt marsh we mimicked defoliation using monthly mowing, and soil compaction, using a rammer, on an annual basis. We quantified the response of soil physical properties, plants and soil fauna, and compared these to cattle-grazed sites at the same salt marsh.

We found that soil physical conditions of the compacted plots were similar to grazed conditions, showing a decrease in soil aeration and increased waterlogging. Soil salinity was increased in all treated plots due to an increase in bare soil. Cover of the tall, dominant grass *Elytrigia atherica*, was decreased in the defoliated plots. However, only when compaction and defoliation were combined, did cover of halophytes increase, as is common on grazed salt marshes. Epigeic arthropods were negatively affected only by defoliation, while abundance of soil microarthropods decreased in the compacted plots, but increased in the exclusively defoliated plots. Conversely, macrodetritivores were not affected by soil compaction, but were absent under grazing.

We conclude that under grazed conditions both soil compaction and defoliation are important drivers of community composition on wet fine-textured soils, although they differ in importance for different groups of organisms. Studying these processes simultaneously is crucial to obtain a better understanding of the effects of large herbivores on plant- and animal communities.

Submitted

INTRODUCTION

Over the last decades there has been an increased interest in the effects of large herbivores on above and belowground community composition (Bardgett and Wardle 2003, Kohler et al. 2004, Mikola et al. 2009, Sørensen et al. 2009). Above ground, large herbivores can affect plant standing crop, ecosystem productivity (Hobbs 1996), plant species composition (Milchunas and Lauenroth 1993, Olff and Ritchie 1998) and arthropod communities (Tscharntke and Greiler 1995, Joern and Laws 2013). Below ground, they affect soil physical conditions (Hamza and Anderson 2005), root exudation patterns (Bardgett and Wardle 2003), mineralisation (Hobbs 1996, Schrama et al. 2013a), and soil biota (Chappell et al. 1971, Bardgett and Wardle 2003). Linking the above- and belowground effects to the actions of large herbivores is, however, not always straightforward.

The actions by which large herbivores affect their habitat are often summarised into three components: defoliation, nutrient return (defecation) and trampling (Trimble and Mendel 1995, Hobbs 2006). Traditionally, defoliation and nutrient return have been viewed as the most important effects herbivores exert on their environment (e.g. McNaughton et al. 1997). Recently, however, effects of trampling have received increasing attention, because they may provide a complementary explanation for the response of plant communities (Sørensen et al. 2009) and soil fauna (Cole et al. 2008, Sørensen et al. 2009, Schon et al. 2010) to grazing, and for processes mediated by soil organisms, such as mineralisation rates (Schrama et al. 2013a, b).

In order to assess the relative importance of these components, proper understanding of the mechanisms by which defoliation, defecation and trampling affect communities is needed. Defoliation affects plant community composition by decreasing light competition and opening of the vegetation to colonisation (Milchunas and Lauenroth 1993, Olff and Ritchie 1998). Moreover, defoliation reduces litter accumulation (Naeth et al. 1991) Aboveground arthropod communities rely heavily on complex vegetation (Morris 1967, Lawton 1983), and are therefore often strongly affected by defoliation (e.g. Gardner et al. 1997, Dennis et al. 2001). Indirectly, the soil fauna can also be affected by defoliation, foremost by an increase in soluble carbon from increased root exudation (Holland et al. 1996, Hamilton and Frank 2001). Defecation increases nutrient availability for plants, increasing primary productivity (Day and Detling 1990) and forage quality (e.g. McNaughton et al. 1997). This can have positive effects on invertebrate abundance, both above (Siemann 1998) and below ground (Curry 1976).

Trampling, on the other hand, can directly kill or damage plants or invertebrates, thereby often increasing litter mass. It also causes compaction of the soil through the application of pressure on the soil surface. This soil compaction decreases pore space and -connectivity and hence transport of oxygen and water (Horn et al. 1995, Hamza and Anderson 2005, Cole et al. 2008). This has been shown to be detrimental to plant productivity (e.g. Lipiec et al. 1991), soil fauna abundance (Chappell et al. 1971, Aritajat et al. 1977, Beylich et al. 2010), nutrient cycling, and can possibly cause changes in plant community composition. It has been hypothesised that this process is especially of importance in fine-textured clay soils, where decreased pore connectivity under wet conditions leads to increased waterlogging and anoxic conditions, and to decreased water infiltration under dry conditions (Liddle 1997, Schrama et al. 2013b).

Disentangling the relative contributions of defoliation and trampling on biota in grazed ecosystems is a major challenge, since trampling and feeding by large herbivores are likely to be spatially correlated. Experimental simulation of these effects can provide insight into their relative contributions, but so far variable results have been reported from different ecosystems (Kohler et al. 2004, Mikola et al. 2009, Olofsson 2009, Sørensen et al. 2009). Because the strongest effects of soil compaction can be expected on fine-textured clay soils, we established a full factorial experiment of defoliation and soil compaction on a temperate coastal salt marsh. We compared communities of plants, epigeic fauna and soil microarthropods between treatments and to those of a nearby grazed marsh.

Western European salt marshes are regularly flooded by sea water and are often grazed by livestock. They feature a distinct zonation of plant and arthropod species, determined by flooding frequency (Adam 1990, Irmler et al. 2002). At the low end of the gradient, inundations occur frequently, and the soil is often waterlogged and anoxic. This zone is dominated by plant species adapted to these saline and anoxic conditions (halophytes). At higher parts of the salt marsh, inundations occur less frequently and here salt-tolerant glycophytic species dominate (Adam 1990). Soil oxygen availability (redox potential) and salinity are the most important abiotic determinants for plant species occurrence in this habitat (Davy et al. 2011) and can both be modified by large herbivores (Esselink et al. 2000, Schrama et al. 2013a). We did not include a fertilizer application treatment because in this high-productive ecosystem nutrient limitation was shown not to play a vital role in determining floristic composition (Bockelmann and Neuhaus 1999).

Starting from an ungrazed situation, dominated by the tall grass *Elytrigia atherica*, we expected that grazed conditions overall would best be approximated by the combined effects of defoliation and soil compaction. With respect to the different biotic groups in our study, we expected the relative importance of the effects to differ between organisms. Specifically, we expected plant community composition to be explained by both defoliation and soil compaction, because plants lose aboveground biomass to defoliation while the roots are affected by soil compaction. Since compaction reduces soil aeration, we expect the halophytic low salt marsh species, adapted to anoxic conditions, to perform well in the compacted soil, at the expense of glycophytes. Epigeic fauna (arthropods living on the soil surface) were expected to be mostly affected by defoliation, because this directly reduces habitat complexity. We hypothesised soil microarthropods to be mostly affected by soil compaction, where especially the larger species were expected to be excluded due to reduced pore space.

MATERIALS AND METHODS

Study site

The study was conducted on a salt marsh at the Dutch Wadden sea coast (Noord Friesland Buitendijks, 53°20'N; 05°43'E; Fig. 1.2). Our study site is a typical mainland salt marsh of anthropogenic origin, resulting from sedimentation fields, with a soil consisting of several meters of marine clay deposits.

Livestock grazing has been common practice on Western European salt marshes for centuries (Bazelmans et al. 2012). At our site, under grazing, several species of grasses and forbs are found in a complex matrix (in order of dominance: *Agrostis stolonifera*, *Plantago maritima*, *Puccinellia maritima*, *Glaux maritima*), while under ungrazed conditions the tall grass E. atherica dominates, interspersed with patches of *A. stolonifera*, *Aster tripolium* and the annual forb *Atriplex prostrata*.

Our experimental plots were located in a long term ungrazed (>25 yr) salt marsh, at a standardised elevation of about 45cm +Mean High Tide (MHT). Average annual rainfall is ca. 800 mm year^{-1} and average inundation frequency at this elevation was 35 inundations year^{-1} over 2008-2010 (Data Rijkswaterstaat). The soil is waterlogged during at least seven months a year, (late August until early April), depending on precipitation, inundations and evapotranspiration.

Experimental design

For our full factorial experiment we chose eight replicate patches (diameter about 6 m) with 100% cover of *E. atherica*. Each of these patches was subdivided into four ca. 1.5 m × 1.5 m plots, leaving where possible >50 cm of untreated vegetation between all plots. Each plot was randomly assigned to one of four treatments: control, defoliation (D), compaction (C), defoliation and compaction (D+C). Root and stolon connections of *E. atherica* were severed along the edge of each experimental plot to 20 cm depth using a knife.

Defoliation was performed by mowing using a brush cutter, preceding the first compaction round in September 2010. Thereafter, mowing was carried out by manually clipping to 5cm above the soil surface at monthly intervals during the growing seasons, (June-September) of 2011 and 2012. Cut plant biomass was removed from the plots.

Compaction was performed using a rammer (Bomag BT60/4; 62 kg, surface 784 cm^2, 13.5 kN, 704 bpm). We walked the rammer three times over the plots at the regular speed of the machine. The total pressure applied to the soil was comparable to 30-50 hoof treads, given a hoof pressure of 220 kPa (Di et al. 2001) and a forward momentum of 2 cm beat^{-1}. Compaction was carried out in October 2010 (wet soil), and thereafter in June 2011 and June 2012 (dry soil) in order to compact sediment deposited by floods over winter.

To compare our treatments to the grazed situation, we chose eight replicate plots, spaced 10 m apart in a grazed salt marsh (stocking density 1 cow ha^{-1}, grazed May to October, for ca. 10 years). These plots were located at the same site, approximately 1 km from the experimental plots, at the same elevation above MHT.

Sampling

SOIL PHYSICAL PROPERTIES

To test the effect of our experimental treatments, we assessed a number of soil physical parameters. We measured bulk density, air filled porosity, soil moisture content and soil organic matter content in June 2011 (seven months after the first compaction round), when the soil was relatively dry, and in September 2011 (four months after the second compaction round) when the soil was waterlogged. We took soil samples in all plots using standardised 100 ml metal rings (pF rings, 5.1 cm height), two samples in June 2011 and one sample in September 2011. Care was taken not to increase soil compaction during sampling. After initial weighing, all samples were saturated with water by increasing the water table of the box in which the rings were kept. The difference between initial weight and saturated weight constituted the air filled volume. Samples were then dried in an oven at 105°C for 48 hours and weighed to determine bulk density and initial water content. Finally, to calculate the percentage organic matter in each sample, ca. $^1/_4$ of the soil core was used to determine total soil organic matter content (including roots) as loss on ignition at 550°C for 3 hours.

We measured soil redox potential, as a proxy for oxygen availability, in the field, using a Graphtec GL200 datalogger with five Pt-electrodes and on HgCl reference electrode following Schrama et al. (2013a) at 2, 5 and 10 cm depth in all plots on September 27th, 2011. Low redox potential is associated with low oxygen availability and the production of toxic compounds, such as H_2S and reduced metals (Laanbroek 1990).

Soil salt concentrations were determined in five (of eight) randomly chosen plots. In each of the plots five 2 cm*2 cm*2 cm soil samples were taken, four from each of the corners and one from the center of the plot. The five samples were mixed by hand. Half of each sample was dissolved in 50 ml demineralised water, after which conductivity was measured using an EC meter (CDM80 Conductivity Meter, Radiometer Copenhagen). The other half was used to determine soil moisture content, by drying soil at 105ºC for 24 h. We used the following conversion to calculate the salt concentration in the diluted sample: $0.4665*(EC^{\wedge 1.0878})$, which assumes that NaCl is responsible for conductivity of the pore water. Afterwards, soil moisture content was used to calculate the dilution factor and the exact salt concentration in the original sample.

PLANTS

We recorded plant species presence and abundance in all plots twice yearly (June and September), from September 2010 until September 2012. Vegetation composition was assessed by estimating cover percentage of each plant species in each of the plots. Nomenclature follows Van der Meijden (2005). We classified the following species as halophytes: *Puccinellia maritima*, *Suaeda maritima* and *Salicornia europaea* (Armstrong et al. 1985), and as glycophytes: *Festuca rubra*, *Agrostis stolonifera*, *Polygonum aviculare* and *Tripleurospermum maritimum*).

In order to assess the effect of compaction on survival of the roots of *E. atherica*, we calculated the proportion of living and dead root and rhizome biomass in the winter following the first compaction treatment. We did this by taking soil cores (Ø10 cm, 20 cm depth), from the centre of each plot and sorting the living and dead roots of *E. atherica*, which were dried in a stove for three days at 70°C and weighed afterwards.

FAUNA

We sampled macrofauna late September 2011, using pitfall traps (Ø10 cm) surrounded by 50cm × 50 cm Perspex enclosures for one week following Schrama et al. (2012). We counted individuals of the crustacean macrodetritivore *Orchestia gammarellus*, and identified all spiders and beetles to species level using Roberts (1995) and Freude et al. (1965-1999), respectively.

We collected soil microarthropods (Collembola and Acari) in June (dry soil) and September (waterlogged soil) 2011 by taking soil cores (Ø10 cm, 10 cm depth) from the center of each of the plots, and divided these into the upper (0–5 cm) and lower (5–10 cm) strata. Soil fauna was extracted using Tullgren extraction (Van Straalen and Rijninks 1982), collected and stored in an ethanol-formaldehyde solution, and identified to species level using Fjellberg (1998, 2007) for Collembola, Weigman (2006) for oribatid mites, Karg (1993) for mesostigmatid mites. Astigmata and Prostigmata were divided over morphospecies, using Hughes (1976) and Krantz and Walter (2009). From the sampling in June we identified fauna from four randomly chosen replicates due to the vast numbers of individuals, and from the sampling in September we identified all fauna from all plots.

Data on average body length were collected for Acari (Karg 1993, Weigmann 2006)) and Collembola (M.P. Berg pers. database). For the morpho-species of the Astigmata and the Prostigmata, we measured a random subset of 12–25 individuals of the more common species from several samples from different depths of the most common species (maximum three individuals per sample). Of the rarer morpho-species, we measured as many as were available. For the common morpho-species we took separate measurements from the June and September sampling rounds, but no significant differences between these periods were found (Appendix 5.1).

Statistical analyses

The relative importance of defoliation and soil compaction for community composition of plants, epigeic fauna and soil microarthropods (0–5 cm depth and 5–10 cm depth separately) were assessed using permutational multivariate analysis of variance (MANOVA) (Adonis in the vegan R library (Oksanen et al. 2013)). We used defoliation, soil compaction and their interaction as factorial explanatory variables. Significance was assessed by permutations of the raw data. These analyses were visualised using non-metric multidimensional scaling (NMDS). We used Bray-Curtis dissimilarities to assess differences in community composition and abundance data were transformed by square root, and standardised using Wisconsin double standardisation. All statistical analyses were done in R 2.15.2 (R Core Team 2012).

SOIL PHYSICAL PROPERTIES

We tested for differences in soil bulk density, soil moisture content and air filled porosity in both the dry period (June) and the wet period (September) using generalised linear mixed models (GLMM; lme4 library (Bates et al. 2013)) with replicate as random and treatment as explanatory variable. Differences in redox potential between treatments were tested using GLMM's with both "replicate" and "electrode" as random factors, and treatment, depth, and their interaction term as explanatory variables. Post hoc linear hypotheses (Tukey tests) were run to test for between level differences using the Multcomp library (Hothorn et al. 2008).

PLANTS

We analyzed the differences in plant community composition (H2) eight months and 24 months after the first compaction. Cover percentages of *E. atherica*, and the combined cover percentage of three short-statured grass species characteristic of grazed salt marshes (*A. stolonifera*, *F. rubra* and *P. maritima*) were compared between treatments. Furthermore, we tested whether halophytes gained higher cover in compacted soil than in uncompacted soil, in comparison to glycophytes. For this, we compared the communities replacing *E. atherica* in all treated plots (one grazed plot with an exceptionally high cover of the halophytic grass *P. maritima* (70%) was excluded from the analysis of halophyte and glycophyte cover). We tested for differences in cover of these functional groups between treatments by fitting GLMM's with a binomial distribution, using replicate as random factor. To correct for over-dispersion we used individual-level random effects. The effect of the treatments on the proportion of dead and live roots of *E. atherica* was similarly assessed, using GLMM's with binomial distributions and replicate as random factor.

FAUNA

We tested differences in the abundance of epigeic fauna and macrodetritivores using Poisson distributed GLMM's with replicate as random factor and treatment as fixed factor. We log-transformed the counts of *O. gammarellus* prior to analysis because of strong heteroscedacity. Post-hoc Tukey tests were used to test for significant differences between treatments.

Differences in abundance and species richness of soil microarthropods (H4) between treatments and depths (0–5 cm; 5–10 cm) were assessed similarly, using Poisson distributed GLMM's with replicate as random factor. Because the two depths taken from each core are likely to be correlated, we also included "core" nested in replicate as random factor. Whenever the interaction between depth and treatment was significant ($p < 0.05$), we split the dataset into the two depths and tested for treatment effects. In order to test whether changes in species richness were a consequence of changes in abundance, we fitted models of species richness explained by treatment, depth and abundance. We used Tukey HSD tests to test for between treatment differences.

To determine whether the average body size of the soil fauna community as a whole was affected by soil compaction, we calculated the community weighted mean (CWM; de Bello et al. 2011) body lengths of both groups, by multiplying the relative abundance of each species with its body length and taking the sum of all species per sample. Because of heteroscedacity in the variance of CWM body length, we used generalised least squares models (GLS) (nlme library (Pinheiro et al. 2012)) with varying variance structures over treatments to test for significant differences between treatments and depths. Although currently no post-hoc analysis is possible for GLS models, we were able to calculate 95% confidence intervals for all pairwise comparisons using the Multcomp library (Hothorn et al. 2008).

RESULTS

Soil physical properties

In June 2011, eight months after the first compaction, air-filled porosity was significantly decreased in the C and D+C plots (by 30%), but also in the D plots (by 13%), and was lowest under grazed conditions (80% lower) ($\chi^2 = 96.43$, $p < 0.001$; Fig. 5.1A). Soil moisture content was increased in C and C+D plots ($\chi^2 = 89.26$, $p < 0.001$; Tukey HSD: $p < 0.001$),

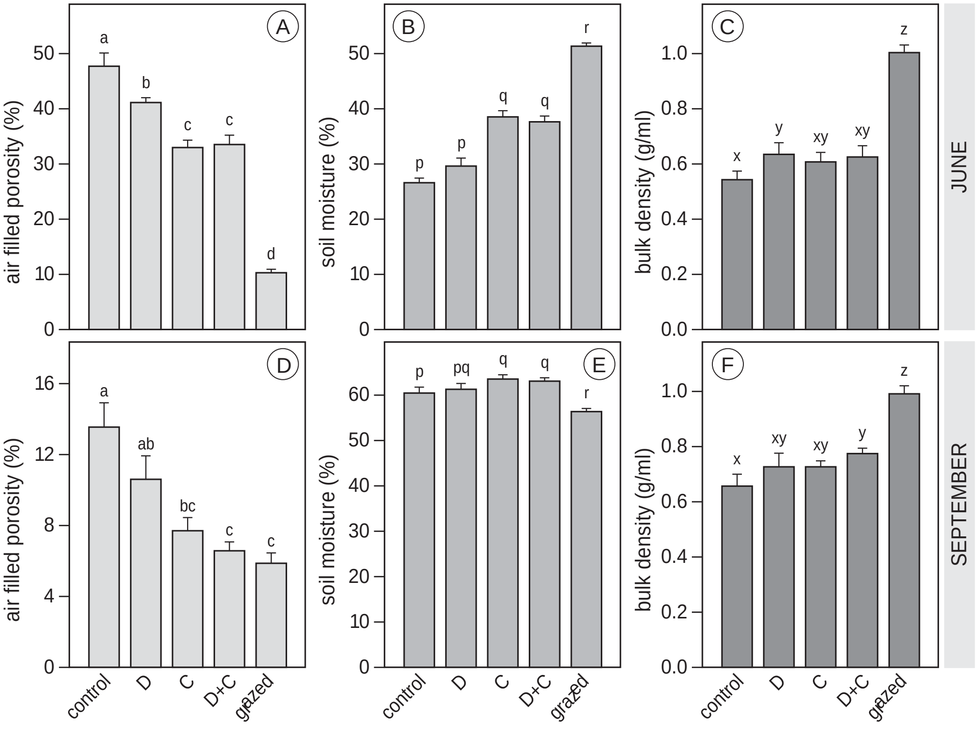

Figure 5.1 Effects of soil compaction (rammer), defoliation (monthly mowing), and long-term grazing (1 cow ha^{-1}) on soil physical properties, on a temperate salt marsh with heavy clay soil. Measurements were taken under dry conditions (June) and waterlogged conditions (September), one year after the start of the experimental treatments. Different letters denote significant differences according to GLMM ($p < 0.05$). D: defoliated, C: compacted, D+C: defoliated + compacted.

but was as still lower than under grazed conditions (Fig. 5.1B). Bulk density, however, was only increased in the D-plots ($\chi^2 = 26.34$, $p < 0.001$; Tukey HSD: $p = 0.03$) and was highest under grazing ($p < 0.001$; Fig. 5.1C).

In September 2011, air filled porosity was decreased and soil moisture was increased in comparison to the June measurements (Fig. 5.1D). Air filled porosity in the C, D+C and grazed plots was almost decreased by half compared to the D and control plots ($\chi^2 = 20.3$, $p < 0.001$). Soil moisture content of the control plots was twice as high as in June. Soil moisture content was significantly higher in C and D+C than in the control plots ($\chi^2 = 26.70$, $p < 0.001$, Fig. 5.1E). Bulk density was increased by 17% in the D+C plots, but was not as high as under grazing ($\chi^2 = 46.16$, Fig. 5.1F). Salt concentration of the pore water was four times higher in the C+D plots than in the control and grazed plots ($p < 0.05$) and almost twice as high as in the C and D plots ($p < 0.001$; Fig. 5.2).

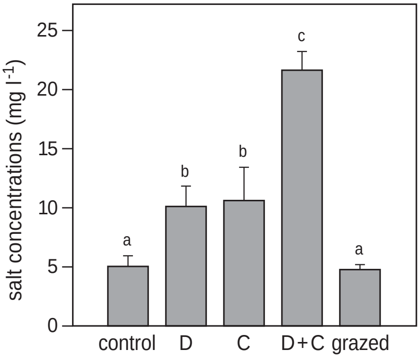

Figure 5.2 Salt concentrations of the soil pore water as affected by defoliation, soil compaction and grazing. Soil samples were taken one year after treatments were applied. D: defoliation, c: soil compaction, D+C: defoliation plus compaction.

Soil redox potential was reduced by more than 100 mV at 2 cm and more than 200 mV at 5 and 10 cm depth in the C, D+C and grazed plots ($\chi^2 = 766.15$, $p < 0.001$), but only by 50 mV in the D plots. The interaction between depth and treatment was significant, and redox potential in the grazed marsh was slightly, but significantly higher than in the D+C plots (Fig. 5.3).

Plants

During the winter following the first compaction, proportion of dead root biomass of the previously dominant grass *E. atherica* was 50% in the D+C plots, which was significantly more than the ca. 10% dead roots found in the control ($\chi^2 = 12.4$, $p = 0.006$, Fig. 5.4). There was no significant effect of the C- or the D-treatments, but the difference between the D- and the D+C plots was marginally significant ($p = 0.053$).

In June, cover of *E. atherica* was severely reduced by D, and even more so by C ($\chi^2 = 83.0$, $p < 0.001$, Fig. 5.5A). After two years, however, *E. atherica* had recovered to ca. 90% of its original cover in the C plots, but cover still tended to be lower than in the control plots ($p = 0.05$). In the D and D+C plots *E. atherica* had decreased to 10–20% cover ($\chi^2 = 47.8$, $p < 0.001$, Fig.5.5A). In contrast, grazing-tolerant short-statured grasses increased over the

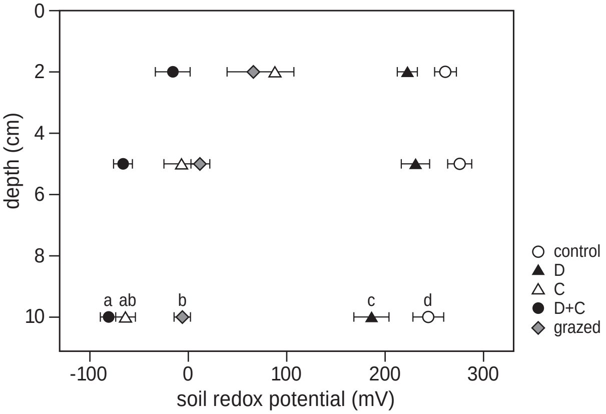

Figure 5.3 Effects of soil compaction, defoliation and grazing on soil redox potential in September 2011 (mean ±se), one year after the start of the experiment. Different letters denote significant differences according to GLMM ($p < 0.05$) in which depth was used as additional random variable. Abbreviations as in Fig. 5.1.

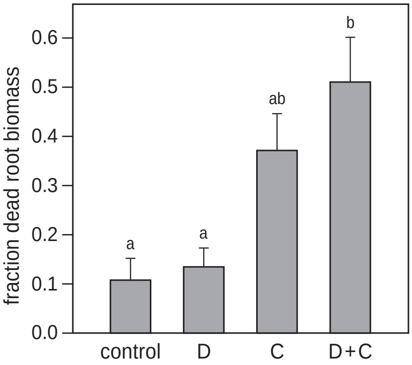

Figure 5.4 Root mortality of *E. atherica* caused by defoliation and soil compaction, 6 months after treatments were applied (March 2011).

course of the experiment. Eight months after compaction there was no difference in the cover of short statured grasses between any of the treatments ($\chi^2 = 1.9$, $p = 0.37$, Fig.5.5B), but after two years significant differences had developed ($\chi^2 = 69.3$, $p < 0.001$, Fig.5.5B). Cover of short-statured grasses in the D plots was now equal to that of the grazed plots (Fig. 5.5B). Bare soil percentage in both the C and the D+C plots was up to 30% eight months after compaction, and up to 60% in the D+C plots after one year. In the D plots, bare soil peaked one year after compaction, reaching on average 27% cover.

There were significant differences in cover of halophytes and glycophytes between treatments (halophytes: $\chi^2 = 18.06$, $p < 0.001$; glycophytes: $\chi^2 = 37.182$, $p < 0.001$; Fig. 5.6). Cover of halophytes in the D+C plots was higher than in the D or C plots (Tukey HSD: $p < 0.001$), and as high as in the grazed plots (Tukey HSD: $P=0.92$). Conversely, glycophyte cover in the D+C plots was lower than in the D or grazed plots (Tukey HSD: $p = 0.003$) but higher than in the C plots (Tukey HSD: $p < 0.001$; Fig. 5.6).

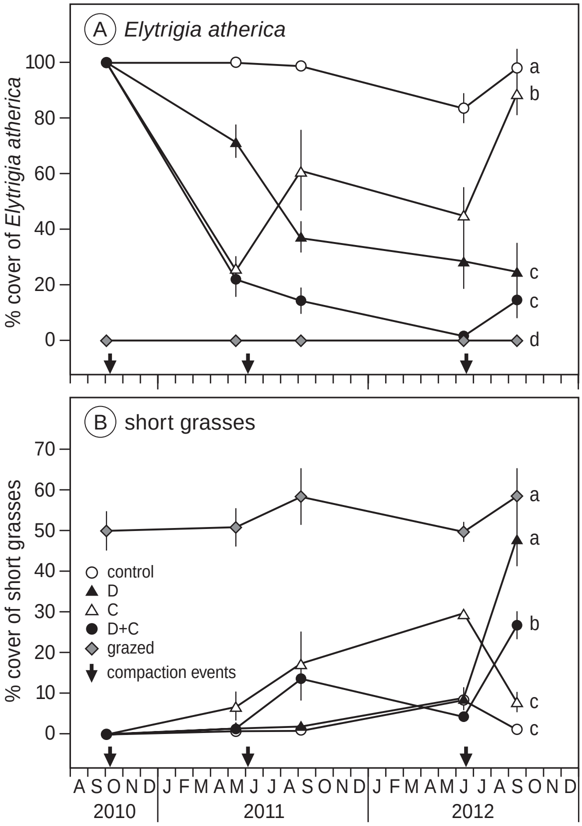

Figure 5.5 Development of average cover percentage of (A) the tall grass E*lytrigia atherica*, and (B) the grazing tolerant short grasses A*grostis stolonifera*, *Festuca rubra* and *Puccinellia maritima* under defoliation, soil compaction (see arrows) and grazing over two years. Different letters denote significant differences in cover percentage after two years, and error bars denote standard errors. Abbreviations as in Fig. 5.1.

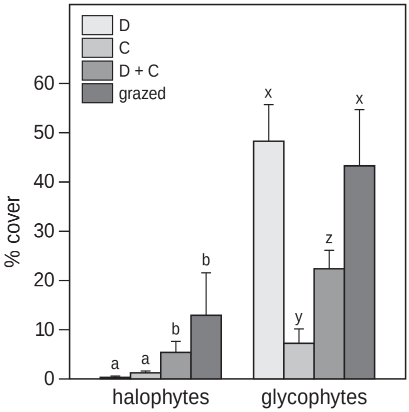

Figure 5.6 Plant communities replacing *E. atherica* in the treated plots, after two years of monthly mowing and three compaction rounds, compared to grazed conditions. Halophytes: *P. maritima*, *S. maritima*, *S. europaea*; Glycophytes: *A. stolonifera*, *F. rubra*, *T. maritimum*, *P. aviculare*; not included: *E. atherica*, *A. tripolium*, *Plantago maritima*, *A. prostrata*. Different letters denote significant differences according to GLMM ($p < 0.05$) and error bars denote standard errors. Abbreviations as in Fig. 5.1.

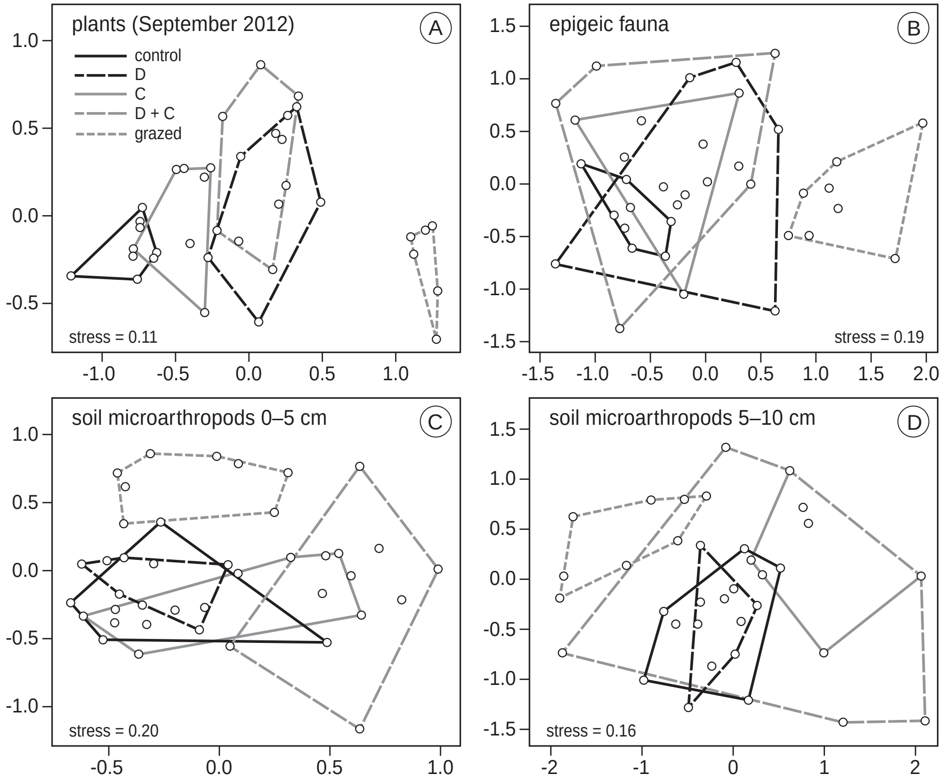

Figure 5.7 Biplots of first two NMDS axes of (A) plants, (B) epigeic fauna (beetles and spiders) and soil microarthropods (Collembola and Acari) at (C) 0–5 cm and (D) 5–10 cm depth in reaction to defoliation (monthly mowing), soil compaction and long-term grazing. Plant species composition was assessed two years, and animal communities one year after the start of the experiment. Abbreviations as in Fig. 5.1.

Table 5.1 Multivariate permutational ANOVA results showing the relative importance of defoliation and soil compaction and their interaction in determining species composition of plants (after two years), epigeic fauna and soil microarthropods (after one year) in a full-factorial experiment of defoliation (monthly mowing) and soil compaction (once yearly). Grazed plots were omitted. 'ns' indicates non-significance ($p > 0.1$), marginally significant factors ($0.05 < p < 0.1$) are shown, but not included in the final models.

	defoliation			compaction			defoliation* compaction		
	F	p	R^2	F	p	R^2	F	p	R^2
Plants	45.05	**<0.001**	0.58	3.28	**0.05**	0.04		ns	
Epigeic fauna	4.21	**<0.001**	0.13		0.09			ns	
Soil microarthropods									
0–5 cm depth		ns		6.56	**<0.001**	0.18		0.06	
5–10 cm depth		ns		5.89	**<0.001**	0.16		ns	

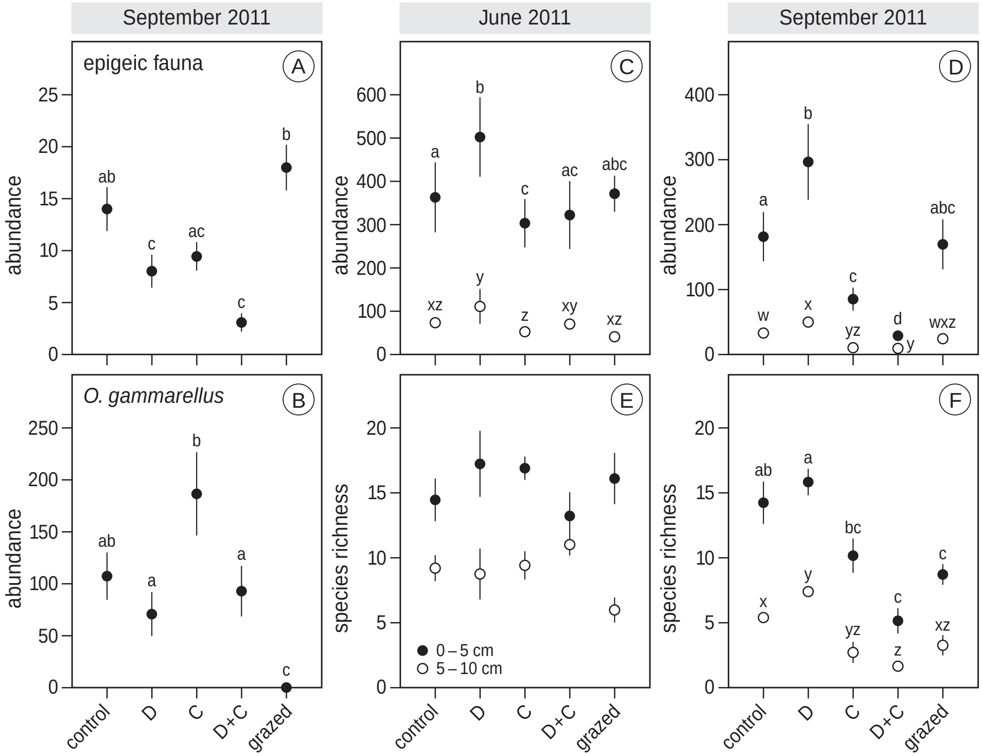

Figure 5.8 Effects of soil compaction, defoliation and grazing on abundance of (A) epigeic fauna (spiders and beetles), (B) the crustacean macrodetritivore *Orchestia gammarellus* and (C-F) abundance and richness of soil microarthropods (Collembola and Acari) (mean ± standard error). Epigeic fauna and macrodetritivores were sampled in September 2011 using enclosed pitfall traps. Microarthropods were sampled by taking soil cores in June 2011 (C, E) and September 2011 (one year after the start of the experiment) (D, F). Different letters denote significant differences according to GLMM ($p < 0.05$) (a-c for 0–5 cm depth, w-z for 5–10 cm depth).

MANOVA of the plant communities two years after the start of the experiment showed that defoliation, soil compaction, and their interaction term explained 62% of plant species composition. Defoliation explained the majority of variation (defoliation $R^2 = 0.58$, compaction $R^2 = 0.04$, Table 5.1). NMDS of plant communities shows the communities of the C and D+C plots to become similar to the grazed plots (Fig. 5.7A).

Fauna

We caught 470 epigeic arthropod individuals in September 2011, represented by 17 species of spiders and 22 species of beetles (Appendix 5.2). Abundance of epigeic fauna was significantly affected by our treatments ($\chi^2 = 72.1$, $p < 0.001$; Fig. 5.8A). Abundance was halved in both the D and the D+C plots, compared to the control (Tukey HSD: $p < 0.001$), but only marginally so in the C plots (ca. 30%, Tukey HSD: $p = 0.054$). Under grazed conditions, however, the abundance of epigeic arthropods was as high as in the control treatment (Fig. 5.8A), but community composition differed considerably from all treatments (Fig. 5.7B). MANOVA showed that communities of epigeic fauna were significantly affected by D (Table 5.1, Fig. 5.7B), but only marginally by C (Adonis: $p = 0.09$).

We caught 16,567 microarthropod individuals, represented by 36 (morpho) species of Acari and nine species of Collembola (Appendix 5.1). In June, soil fauna were more numerous than in September (9519 individuals vs. 7048 individuals), but most species were found in both periods and in both the experimental area and the grazed marsh. Abundances per species differed between sampling periods and treatments.

Species richness and abundance of soil microarthropods were significantly lower at 5–10 cm depth than at 0–5 cm, during both periods, in all treatments (GLMM: $p < 0.001$, Fig. 5.8C-F). In June, the abundances were decreased by a third in the C and D+C plots, and increased by a third in the D plots (0–5 cm: $\chi^2 = 246.2$, $p < 0.001$; 5–10 cm: $\chi^2 = 92.0$, $p < 0.001$; Fig. 5.8C), but there was no difference in species richness between any of the treatments at either depth (0–5 cm: $\chi^2 = 3.1$, $p = 0.54$; 5–10 cm: $\chi^2 = 6.0$, $p = 0.20$, Fig.5.8E).

In September, however, there were strong effects of soil compaction both on species richness (0–5 cm: $\chi^2 = 2483.1$, $p < 0.001$; 5–10 cm: $\chi^2 = 413.7$, $p < 0.001$) and abundance (0–5 cm: $\chi^2 = 32.4$, $p < 0.001$; 5–10 cm: $\chi^2 = 23.2$, $p < 0.001$) of soil microarthropods (Fig. 5.8D,F). In the upper layer, abundance was increased by half in the D plots, but decreased by more than 80% in the D+C plots. In the deeper layer, both abundance and richness decreased by about 75% (Fig. 5.8D,F). Incorporation of abundances in the models explaining species richness showed only a significant difference between the grazed and the control plots in the upper layer, and in the deeper layer only a marginal difference between the D and D+C plots (Tukey HSD: $p = 0.04$). This indicates that differences in species richness are mostly explained by differences in abundances.

MANOVA showed that soil compaction was a highly significant factor in explaining community composition of soil microarthropods (Table 5.1), but the interaction between defoliation and compaction was marginally significant for the upper stratum ($p = 0.059$). Explanatory power of the models, however, was low (0–5 cm: $R^2 = 0.18$; 5–10 cm: $R^2 = 0.16$). NMDS of the microarthropod communities in September showed the high similarity between the control and the D plots, and a shift in composition due to soil compaction (Fig. 5.7C,D), while the grazed plots were distinctly different from all other plots.

CWM body length was significantly lower in the deeper soil layer than in the upper layer for both Acari and Collembola (GLS: $p < 0.001$, Table 5.2). However, only in the D+C plots a 30% smaller CWM body length was observed compared to the D plots in June (GLS: $p < 0.05$, Table 5.2). Collembola were virtually absent in the deeper layer of the C and D+C plots (present in only 4 out of 16 compacted plots) in September (Table 5.2). The CWM body length of Collembola was twice as high under grazed conditions as under any other treatment (GLS: $p < 0.05$). This was driven by the high proportional abundance of the large species *Isotoma riparia*. The macrodetritivore *O. gammarellus* was twice as abundant in the C plots as in either of the defoliated treatments (Tukey HSD: $p = 0.01$, Fig. 5.8B). Under grazed conditions this species was, as expected, virtually absent.

DISCUSSION

This study aimed at separating the effects of defoliation and soil compaction on plants, epigeic fauna and soil microarthropods on fine-textured clay soil. Our results show that both compaction and defoliation play a crucial role in explaining the effects that large herbivores exert on abiotic soil conditions and on biotic communities on this wet clay soil. We detected strong species sorting in plant communities, but only weak patterns in the more mobile animal communities. These differences may have both spatial and temporal causes. It can be expected that over time, the defoliated and compacted plots will become more similar to grazed salt marshes. Nevertheless, on the limited spatial and temporal scale of the present experiment we were able to successfully distinguish the different drivers for different functional groups.

We had hypothesised that a combination of defoliation and soil compaction would best simulate grazed conditions, and found varying support for different biotic groups: soil physical properties under grazing were well approximated by our compaction treatment. Under defoliation, on compacted soil, plant species composition showed a clear directional change towards the composition under grazed conditions. This was mostly explained by defoliation and to a minor extent by soil compaction. Abundance of epigeic arthropods was detrimentally affected by defoliation, but not by soil compaction. Under none of the treatments, however, did arthropod community composition resemble the

Table 5.2 Effects of soil compaction, defoliation (monthly mowing) and grazing on community weighted mean body length (mm) of Collembola and Acari under dry (June 2011) and waterlogged (September 2011) conditions. Soil fauna was collected from soil cores using Tullgren-extraction. D: defoliated, C: compacted, D+C: defoliated + compacted, NA: not calculated due to absence in most samples.

		Treatment				
		Control	D	C	D+C	Grazed
June 2011						
Collembola	0–5 cm	1.27(±0.23)ab	2.83(±0.60)a	1.83(±0.34)ab	0.93(±0.13)b	2.76(±0.68)ab
	5-10 cm	0.99(±0.05)a	1.05(±0.06)a	0.72(±0.01)a	1.05(±0.13)ab	0.93(±0.06)b
Acari	0–5 cm	0.39(±0.01)a	0.41(±0.01)a	0.40(±0.02)a	0.39(±0.01)a	0.41(±0.02)a
	5–10 cm	0.36(±0.03)ab	0.38(±0.02)a	0.29(±0.03)ab	0.36(±0.01)a	0.33(±0.02)b
September 2011						
Collembola	0–5 cm	3.16(±0.64)a	3.23(±0.46)a	2.11(±0.38)a	2.08(±0.68)a	5.59(±0.17)b
	5–10 cm	1.07(±0.22)a	0.88(±0.04)a	NA*	NA**	1.07(±0.33)a
Acari	0–5 cm	0.48(±0.02)ab	0.44(±0.02)ab	0.41(±0.02)a	0.42(±0.02)a	0.58(±0.05)b
	5–10 cm	0.35(±0.07)a	0.29(±0.03)a	0.23(±0.01)a	0.32(±0.05)a	0.32(±0.07)a

*absent in 5/8 of samples

** absent in 7/8 samples

community found under grazed conditions. Surprisingly, abundance of soil microarthropods was detrimentally affected by our soil compaction treatment, but not by grazing, while the macrodetritivore *O. gammarellus* showed the opposite pattern.

Soil physical properties

Soil compaction caused a decrease in air-filled porosity, soil moisture content and redox potential, while increasing bulk density and salt concentrations. Air filled porosity and redox potential are strong determinants of plant species composition (Davy et al. 2011) and were similar between the compacted and the grazed plots, especially during the wet period. The increase in bulk density, however, was not sufficient to reach values comparable to the grazed reference site. This may partially be explained by our compaction treatment being rather modest compared to long-term trampling by large herbivores, and secondly by a higher sand fraction present at the grazed marsh (47% at the grazed marsh vs. 27% at the experimental location (S. Nolte, unpublished data)). Sand has a higher mass density than clay and therefore leads to higher bulk densities. Nevertheless, overall soil physical conditions of grazed marshes were well approximated by our compaction treatment.

An additional abiotic effect of both soil compaction and defoliation was an increase in salt concentrations up to four times the levels of the control and the grazed conditions. Grazing has been shown to often cause increased salinity, both in salt marshes (Bakker et al. 1985, Srivastava and Jefferies 1996, Esselink et al. 2000), and in arid systems (Lavado and Taboada 1987, Chaneton and Lavado 1996). This is generally assumed to be caused by an increase in bare soil percentage and subsequent surface evaporation of salt water (Lavado and Taboada 1987, Srivastava and Jefferies 1996). We hypothesize that increased waterlogging due to soil compaction reinforces this process, especially on fine textured soils. Our defoliation and soil compaction treatments therefore had a dual effect: 1) a decrease in above ground biomass, leading to increased proportions of bare soil, and 2) a decrease in water infiltration, leading to water logging of sea water and the accumulation of salt at the soil surface after evaporation of water. These high salt concentrations can explain the increase in halophyte cover in our compacted plots, which has also been reported from other salt marshes where grazing has been reinstated (Bakker 1985, Esselink et al. 2000). This is deemed positive for the conservation value of this threatened habitat type.

Plants

We hypothesised that plant species composition would be determined by both defoliation and soil compaction and found support for this hypothesis, although defoliation was much more important in determining plant species composition than soil compaction. Other experiments aiming at disentangling the effects of defoliation and trampling on plant communities showed either a major role for trampling, and no effect of defoliation (Sørensen et al. 2009), or weak effects of both (Kohler et al. 2004). In contrast, Mikola et al. (2009) found strong evidence for the importance of defoliation in improved agricultural grasslands, because it controlled cover of the competitive dominant *E. repens*, a congeneric of *E. atherica*. In our experiment, we found large effects of both soil compaction and defoliation on various biotic groups. This difference may be explained by the fact that we started from an ungrazed situation, and performed this experiment on readily compactable clay soil characteristic of this ecosystem. This corroborates earlier findings that effects of soil compaction may be especially important in fine-textured soils (Schrama et al. 2013a,b).

As we had anticipated (Bakker 1978, Veeneklaas et al. 2011), *E. atherica* was not able to persist under defoliation, and was also absent from the grazed salt marsh, but it appeared well able to persist under soil compaction in absence of defoliation. After an initial decrease in cover, this species rapidly recovered in the C plots, until almost complete cover was re-established two years after the start of the experiment. E*lytrigia atherica* is normally restricted to well-aerated sites on the higher salt marsh (Armstrong et al. 1985, Davy et al. 2011), but our results, and those of others (Bockelmann and Neuhaus 1999), show that this species is well capable of colonising and persisting in areas that are waterlogged most of the year. We hypothesize that this can be attributed to plasticity in forming aerenchyma in the roots, and quick regrowth from belowground storage organs. The combination of regular trampling and defoliation, however, seems to be detrimental to this species, explaining its low abundance in the defoliated + compacted plots as well as at the grazed marsh.

As hypothesised, we also found support for higher abundance of halophytes under combined soil compaction and defoliation than under defoliation alone. The presence of halophytes on the higher zone of grazed salt marshes is often reported (Bakker 1978, Bakker et al. 1985, Schröder et al. 2002). It has been suggested that halophytes are able to colonize this zone under grazed conditions because of zoochorous dispersal and decreased light competition (Bakker et al. 1985). Instead, our results suggest that soil compaction and the associated decrease in soil aeration and increase in salinity, together with defoliation, created conditions similar to the lower salt marsh. This may allow halophytes to compete with species typical for higher salt marsh, thereby extending their range (see also Esselink et al. 2000).

Yet, two years was not enough to make plant community composition of our experimental plots equal to that of the long-term grazed marsh. Several short-statured plant species that commonly occur under grazed conditions had not colonised our treated plots. It therefore seems that an equilibrium state had not yet been reached. Indeed, when comparing vegetation in our treated plots to adjacent salt marshes where grazing was installed three year previously (S. Nolte unpublished data), an obvious similarity with the D+C plots becomes apparent, whereas the D plots appear distinctly different (Fig. 5.9). This suggests that, although abiotic conditions of a grazed march were adequately mimicked by our treatments, the associated plant community assembles much slower.

Fauna

As we hypothesised, species composition of epigeic arthropods was affected by defoliation, but not by soil compaction. Previous studies have shown an important role for vegetation structure in explaining effects of large herbivores on beetle and spider communities

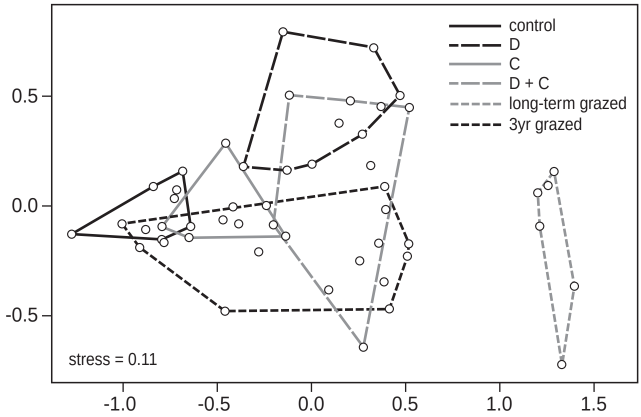

Figure 5.9 NMDS biplot of plant communities (based on estimated cover percentage of all species) two years after the start of the experimental treatments (defoliation and soil compaction) and adjacent salt marshes where grazing was instated three years previously.

(e.g. Gardner et al. 1997, Dennis et al. 2001), but these were not able to separate the effects of soil compaction and defoliation. Hofmann and Mason (2006) reported some rove beetle species to be associated with compacted soil, but we were not able to confirm these findings, possibly in part due to the relatively low abundances of rove beetles during sampling in September.

Although soil physical properties were similar between the grazed and compacted plots, the effects on soil microarthropods differed strongly. In line with our expectations, soil compaction caused a decrease in abundance of soil microarthropods, but, surprisingly, grazing did not, despite the similarities in soil physical conditions. Detrimental effects of soil compaction on microarthropods are often reported in literature, both under grazed conditions (e.g. King and Hutchinson 1976, Petersen et al. 2004, Schon et al. 2010) and under crop production (e.g. Aritajat et al. 1977, Heisler 1994, Schrader and Lingnau 1997). However, positive effects of grazing on the abundance of microarthropods have also been reported (Bardgett et al. 1993), and were attributed to an increased availability of soluble C and N.

Our contrasting results of experimental soil compaction and grazing may be explained by the short duration of the experimental treatments. Our compaction treatments caused a sudden change in abiotic conditions by collapsing all habitable pore space, whereas grazing was stable for over two decades. Long-term stability may have led to the formation of stable soil aggregates and small air pockets due to root turnover. In addition, grazing may lead to more favorable conditions for soil fauna as a result of increased nutrient input due to defecation, radial oxygen loss, root exudation and greater root penetration (Bardgett and Wardle 2003). It is thus reasonable to assume that, on the long term, a new equilibrium will establish, allowing re-colonisation by soil fauna when plants roots (again) penetrate these lower strata.

In contrast to the detrimental effects of compaction, defoliation had an unexpected positive effect on the abundances of microarthropods, both in the dry and the wet period. Effects of defoliation on soil fauna reported by other researchers are as variable as grazing effects (positive: Jensen et al. (1973), Seastedt et al.(1988); neutral: Butenschoen et al. (2008); negative: Schon et al. (2012)). We hypothesize that short-term increases in root exudation, an increase in soil temperature, and/or decomposition of high quality litter may have caused an increase in soil fauna, despite our efforts to remove all cut biomass. On the long term, the positive effects of defoliation on microarthropods may counterbalance the negative effects of soil compaction, explaining the lack of effects of grazing.

While we expected the macrodetritivore *O. gammarellus* to be negatively affected by soil compaction, our results showed the opposite. *Orchestia gammarellus* occurs at high densities in ungrazed, late successional salt marshes (Meyer et al. 1995, Schrama et al. 2013a). Since other macrodetritivores are known to react negatively to a decrease in pore space and an increase in anoxic conditions (e.g. Piearce 1984), we expected soil compaction to be the main driver of macrodetritivore abundances in salt marshes. The lack of negative effects of soil compaction may be explained the small plot size. This species is able to cover distances up to 12 meters per night (M.P. Berg, unpublished data.), it therefore is probable that recolonisation of the treated plots from the surrounding vegetation has occurred. The individuals found in the compacted plots may have been driven out of the favorable patches due to intraspecific competition, or may have been attracted by some unknown property of the C-treatment. Indeed, it is not unlikely that an increase in resource abundance (fresh dead organic matter of high quality), due to the compaction treatment, may have created a favorable habitat. It therefore appears that compacted soil is not the main determinant for the absence of *O. gammarellus* in grazed salt marshes, and that presence of nearby tall vegetation and/or a thin litter layer may be sufficient for this species to colonize grazed patches.

We found very limited support for the hypothesised decrease in averaged body size of microarthropods. Soil fauna was generally smaller in the deeper soil layers of all treatments, but it seems that most of these species are able to survive under compacted conditions. A sharp decrease in abundance and richness was evident, especially under waterlogged conditions. This was accompanied by a shift in composition of the microarthropod community, since in the lower soil strata Collembola disappeared almost completely under soil compaction, whereas several species of Acari were still present. Collembola therefore seem to be more sensitive to soil compaction than the smaller-sized Acari, as was also found in other studies (King and Hutchinson 1976, Aritajat et al. 1977, Heisler 1994).

Epigeic predators such as spiders and ground- and rove beetles could be expected to react to changes in abundance of their main prey, Collembola (Schaefer 1974, Wise et al. 2006). Yet, the strong decrease in microarthropod abundance caused by soil compaction was not reflected in the abundance of epigeic fauna, nor was the increased abundance in the D-plots matched. This suggests that vegetation structure is a stronger determinant of epigeic predator abundance and species composition than prey abundance.

Conclusions

Separating the effects of defoliation and trampling is methodologically challenging, since the exact actions of large herbivores are not easily mimicked. Large herbivores often return to feeding stations at regular intervals (McNaughton 1984), and therefore exert pressure on the soil repetitively. Our compaction treatment attempted to mimic this using a rammer with the approximate equivalent of 30–50 treads per year, on a single day. Although this pressure is severe for a single day, it was probably comparatively low on an annual basis, as high visitation rates of large herbivores may be expected in productive ecosystems such as salt marshes. Nevertheless, we were able to create soil conditions similar to those encountered on long-term grazed marshes, suggesting our treatment was successful. Obviously, we were not able to approximate the large-scale, long-term interplay of soil compaction, bioturbation, sedimentation, and species turnover. To fully understand these complex interactions, experiments at scales temporally and spatially similar to those at which large herbivores operate are necessary.

Soil compaction and defoliation have different, often even opposite effects on the above- and belowground biota. Plant communities reacted to both treatments, but defoliation was much more important than compaction. Epigeic fauna was only responsive to defoliation, but not to compaction, whereas for soil microarthropods only soil compaction determined community composition to a large extent. Because soil fauna is important in decomposition and mineralization processes (Seastedt 1984), low abundance and diversity of soil fauna can explain observations of decreased mineralization (Kiehl et al. 2001, Schrama et al. 2013a), reduced decomposition (Ford et al. 2012) and increased carbon sequestration (K. Elschot unpublished data) in grazed salt marshes. We conclude that herbivore-induced soil compaction should be seen as an additional mechanism explaining herbivore-induced changes in plant and soil fauna communities. A key challenge for the future will be to address the temporal and spatial dynamics of this effect and to address these issues in other grazed systems.

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Appendix 5.1 Species list with body length measurements of Acari or literature values of Acari and Collembola

species	size (mm)	Standard deviation (mm)	n	source
Acari				
Astigmata				
Histiostoma	0.23	0.010	3	measured
Rhyzoglyphus	0.35	0.032	8	measured
Tyrophagus (June)	0.41	0.071	10	measured
(September)	0.37	0.092	17	measured
Oribatida				
Liebstadia similis	0.60			Weigman 2006
Oribatella litoralis	0.45			Weigman 2006
Ramusella insculpta	0.30			Weigman 2006
Prostigmata				
Bdella	1.19	0.277	5	measured
Bdella sp2	0.45		1	measured
Erythraeus	0.80	0.145	4	measured
Eupodes (June)	0.334	0.040	12	measured
(September)	0.338	0.045	12	measured
Leptus spec	0.52	0.037	5	measured
Pygmephorus (June)	0.227	0.008	12	measured
(September)	0.224	0.025	9	measured
Rhagidia	0.64	0.054	6	measured
Scutacarus	0.18	0.017	14	measured
Stigmaeidae	0.34	0.023	18	measured
Tarsonemus	0.14	0.017	5	measured
Trombidiidae	1.49		1	measured
Trombidiidae 2	1.81		1	measured
Tydeus	0.28	0.025	6	measured
Mesostigmata				
Amblyseius spec.	0.37			Karg 1993
Cheiroseius salicorniae	0.6			Karg 1993
Geholaspis mandibularis	0.77			Karg 1993
Hypoaspis aculeifer	0.51			Karg 1993
Lasioseius cf. berlesei	0.44			Karg 1993
Lasioseius confusus	0.57			Karg 1993
Leioseius bicolor	0.495			Karg 1993
Lysigamasus vagabundus	0.8			Karg 1993
Macrocheles spec	0.63			Karg 1993
Neojordensia laevis	0.46			Karg 1993
Pachylaelaps siculus	0.58			Karg 1993
Parasitus spec.	0.83			Karg 1993
Pergmasus crassipes	1.22			Karg 1993
Phytoseiidae	0.375	0.016868	2	measured
Uropoda orbicularis	0.72			Karg 1993
Collembola				
Folsomia sexoculata	2.1			Fjellberg 2007
Friesea truncata	1.0			Fjellberg 1998
Halisotoma maritima	1.7			Fjellberg 2007
Isotoma riparia	6.0			Fjellberg 2007
Mesaphorura macrochaeta	0.7			Fjellberg 1998
Sminthurinus aureus	1.0			Fjellberg 2007
Sminthurus nigromaculatus	3.0			Fjellberg 2007
Sphaeridia pumilis	0.5			Fjellberg 2007
Thallassaphorura debilis	1.4			Fjellberg 1998

Appendix 5.2 Species composition of epigeic fauna (spiders and beetles) one year after the start of the experiment (late September 2011). Animals were caught using pitfall traps enclosed in 50 cm*50 cm Perspex enclosures for a one week period. D: monthly defoliation; C: yearly soil compaction, D+C: both defoliation and soil compaction.

	Control	D	C	D+C	Grazed	Total
Araneae						
Allomengea scopigera	30		23			**53**
Argenna patula		1				**1**
Bathyphantes gracilis	6	4	3	1	1	**15**
Centromerita bicolor	2					**2**
Erigone longipalpis		3	2	1	121	**127**
Hypomma bituberculatum					1	**1**
Leptorhoptrum robustum	15	1	2			**18**
Oedothorax apicatus		1				**1**
Oedothorax fuscus		3		1	6	**10**
Oedothorax retusus	3	16	5	2	8	**34**
Pachygnatha clercki	22	7	22	7	2	**60**
Pardosa purbeckensis	10	8	5	1		**24**
Pirata piraticus			1	2		**3**
Robertus arundineti	4	9				**13**
Stemonyphantes lineatus		1	1			**2**
Trochosa ruricola	2		1			**3**
Walckenaeria kochi			1		1	**2**
Total Arraneae	**94**	**54**	**66**	**15**	**140**	**369**
Coleoptera						
Acrotona amplicollis		1				**1**
Amara aenea	1					**1**
Amischa analis				2		**2**
Atomaria nigrirostris					1	**1**
Atomaria rhenana	1					**1**
Bembidion aeneum	3		1	1		**5**
Bembidion minimum		1	1	1		**3**
Brachygluta helferi	1					**1**
Brundinia marina	2	1		1		**4**
Cercyon analis	1					**1**
Cercyon melanocephalus				1		**1**
Chaetocnema concinna		1				**1**
Coccinella septempunctata	1					**1**
Dicheirotrichus gustavi					1	**1**
Glischrochilus hortensis			1	1		**2**
Helophorus brevipalpis	1	3	3			**7**
Ischnopterapion virens		1				**1**
Ochthebius auriculatus	2	1	3	1		**7**
Quedius semiaeneus					1	**1**
Quedius simplicifrons	5					**5**
Tachyporus atriceps		1				**1**
Xantholinus longiventris					1	**1**
Total Coleoptera	**18**	**10**	**9**	**8**	**4**	**49**
Grand Total	**112**	**64**	**75**	**23**	**144**	**418**

Chapter 6

Effects of livestock species and density on flower-visiting insects in a salt marsh

Roel van Klink, Jan P. Bakker, Michiel F. WallisDeVries

ABSTRACT

On European coastal salt marshes, livestock grazing is an efficient conservation measure to maintain botanical diversity and structural heterogeneity, which could also benefit flower-visiting insects. The optimal grazing regime for maintaining both plant and insect species richness remains to be determined, however. We set up a triplicate grazing experiment with five treatments at a salt marsh along the Dutch Wadden Sea coast: two livestock species (cattle and horses), each at two stocking rates at (0.5 and 1 animal ha^{-1}) and rotational grazing (rotation with 1 cow/ha in one year and no grazing in the other year).We measured the effects of these grazing treatments on floral resources and flower-vising insects (day-active butterflies, hoverflies, honey bees and bumblebees).

Total flower abundance was not affected by continuous grazing, but the abundance of Asteraceae was significantly lower at high stocking densities. Flower visitors were also most abundant at low densities, but we found no differences between cattle and horse grazing. The abundance of flower visitors per paddock was well explained by the abundance of Asteraceae flowers, when corrected for year effects. Preliminary analysis of 1.5 rotational cycles showed that flower-visiting insects are most abundant under rotational grazing, which was especially evident during the ungrazed year.

Our results indicate that for flower-visiting insects on salt marshes, grazing by cattle or horses at a density of 0.5 animal ha^{-1} is to be preferred over higher densities. Rotational grazing seems to be even more beneficial to flower-visiting insects, but its long-term consequences on flower abundance require further study.

INTRODUCTION

Coastal salt marshes are rare and threatened ecosystems that harbour a host of plant and invertebrate species that are confined to this habitat. On the salt marshes of Western Europe, biodiversity of especially plants (Bakker et al. 2003) and their associated insect herbivores (chapter 4) is threatened by the encroachment of the tall, dominant grass species *Elytrigia atherica*. To reduce or prevent the dominance of *E. atherica* and the subsequent loss of biodiversity, livestock grazing is an important management option (Bakker et al. 2003). It is currently unclear, however, what the optimal grazing management is for plant and insect conservation with respect to stocking density and livestock species.
Traditionally, livestock on the Dutch salt marshes were cattle, but recently horse grazing has become increasingly popular, with unknown implications for the flora and fauna. Another potentially valuable management option is rotational grazing, where grazed years are alternated with ungrazed years. This type of management has been coined to be especially useful for insect conservation (see chapter 2).

Here, we study the effects of different stocking densities and livestock species (cattle or horses) and rotational grazing with cattle on the abundance of flower-visiting insects. Flower-visiting insects perform important roles in ecosystems as pollinators, and, in the case of hoverflies, also as predators (Chambers 1986). Generally, there is a negative relationship between stocking density and the abundance and richness of arthropods (chapter 2). Hence, abundance and richness of flower-visiting insects and other arthropods are usually found to be highest in ungrazed grasslands (e.g. Kruess and Tscharntke 2002a,b, Pöyry et al. 2004), especially in the first years after cessation of grazing (Balmer and Erhardt 2000, Öckinger et al. 2006), indicating the potential benefits of rotational grazing systems. Some notable exceptions, where flower-visiting insects were found to be most abundant and diverse under high stocking densities, have, however been published (Vulliamy et al. 2006, Yoshihara et al. 2008). The highest pollinator densities are usually associated with the highest abundance and diversity of floral resources, regardless whether these are found under low or high stocking densities (Vulliamy et al. 2006, Yoshihara et al. 2008, Sjödin et al. 2008, Franzen and Nilsson 2008, Batáry et al. 2010).

Knowledge about the potential effects of differences between livestock species on arthropod communities is sparse, however. Species and breeds of large herbivores may differ in body size, mouth morphology or digestive system and activity patterns, and this has a large impact on diet composition (Gwynne and Bell 1968, Jarman 1974). Plant communities have been shown to respond to these herbivore characteristics in terms of spatial patterning (Laca et al. 2010) and species composition, both in natural herbivore assemblages (Veblen and Young 2010) and semi-natural settings (reviewed by Rook et al. 2004). Hence, an effect can be expected on the arthropod fauna, but evidence is very limited. Some tentative indications have been presented showing that cattle grazing has more positive effects on abundance of flower-visiting insects than grazing by the more selective sheep (Carvell 2002, Öckinger et al. 2006), but no difference was observed between cattle and horse grazing (Öckinger et al. 2006) or different cattle breeds (WallisDeVries et al. 2007).

To shed light on the effects of horse and cattle grazing at different stocking densities and the effects of rotational grazing on salt marshes, a grazing experiment was set up at the Dutch Wadden Sea coast in 2010. In this experimental setup we tested the following hypotheses: (1) abundance of flowers and flower-visiting insects will be higher at low than at high stocking densities; (2) there is no difference in the grazing impact of horses and cattle at the same stocking densities; (3) resource abundance is the most important predictor for the abundance of flower-visiting insects. In our system, the tall, mass-flowering Asteraceae *Aster tripolium* and *Cirsium arvense* are expected to be the most important floral resources; (4) we expect especially positive effects of rotational grazing during ungrazed years. However, because the rotational cycle was only completed 1.5 times, the effects of this regime can only be explored preliminarily.

METHODS

Site description

The study was conducted at a mainland salt marsh at the Dutch Wadden Sea coast (53° 20_N 5° 43_E). The site is a typical man-made salt marsh, arising from sedimentation fields and extensive ditching, but is now under nature protection and part of the Wadden Sea World Heritage. The location where the experiment was undertaken displays a clear zonation from the upper parts at the landward side to the intertidal flats. Regarding flower abundance, the higher parts are dominated by *Potentilla anserina* (Rosaceae) and *Tripleurospermum* (formerly known as *Matricaria*) *maritimum* and *Cirsium arvense* (Asteraceae), whereas at the lower parts *Aster tripolium* (Asteraceae) is the most abundant flowering plant. The prostrate *Glaux maritima* (Myrsinaceae) and *Spergularia* spp. (Caryophyllaceae) are present along the entire elevation gradient.

Experimental setup

At this site we set up a grazing experiment in 2010. Five different treatments were installed in three replicate blocks: cattle grazing at high (1 animal ha^{-1}) and low (0.5 animal ha^{-1}) densities, horse grazing at high (1 animal ha^{-1}) and low (0.5 animal ha^{-1}) densities, and rotational grazing (alternately ungrazed and cattle-grazed years (1 cow ha^{-1})) (Fig. 6.1). Two of the replicate blocks started from a grazed situation, whereas one block was ungrazed for some 20 years prior to the start of the experiment and was grazed down intensively prior to the experiment in 2009. Each experimental paddock had a size of 10–11 ha and was grazed May–October annually. Grazing treatments were allocated randomly to each of the five paddocks in each block, with the restriction that no horse-grazed treatments were allowed in adjacent paddocks, as horse herds are expected to influence one another. A fresh water source was present in each paddock at the landward side.

Data collection

We laid out 500 m transects diagonally through each of the experimental paddocks, start-

Figure 6.1 Map of the experimental setup on the salt marshes of Noord Friesland Buitendijks. Grazing treatments are indicated by density ha^{-1} and livestock species (H = horse, C = cattle, R = rotational grazing, N = ungrazed). The freshwater source is marked with a white dot.

ing at the landward side. Along these transects we collected data on abundance of floral resources and flower-vising insects using a modified version of the Pollard walk (Pollard 1977). We counted all Macrolepidoptera (day-active butterflies and moths) by walking along each transect at moderate speed and counting all specimens within a 5 m × 5 m × 5 m cube. Every 25 metres we stopped for one minute and estimated flower abundance in a 2m × 2m square for every plant species on a simple scale: 1: 1–10; 2: 10–50; 3: 50–100, 4: >100 (see also Wallisdevries et al. 2012), and counted all flower-visiting insects (Macrolepidoptera to species level, bumblebees, honeybees and hoverflies counted at family level). This was done in all paddocks three times in 2011-2013: early June, mid-July and late August/early September. Nomenclature follows van der Meijden (2005) for plants and Settele et al. (2008) for butterflies.

Statistical analyses

All statistical analyses were done in R 3.0.1 (R Core Team 2013) using the lme4 (Bates et al. 2013) and Multcomp packages (Hothorn et al. 2008). For statistical analysis, all counts of flowers and insects were pooled per paddock per year. We first compared abundance of flowers and insects in the four continuously grazed treatments using Poisson-distributed linear mixed models (GLMM). We used livestock species (cow/horse) and density (0.5 / 1 animal ha^{-1}) as explanatory variables and year and paddock nested in replicate as random factors. We applied backward model selection to derive a final model, which was then tested for significance in comparison to a model without explanatory variables using the 'anova' command in R. Differences between all four treatments were assessed post-hoc by Tukey tests. Significance was derived by residual maximum-likelihood estimation.

We tested the relationship between the abundance of flowers and flower-visiting insects by simple linear regression on the log-transformed yearly total abundance per paddock of all four treatments, with year (factorial) as covariate. A priori, we expected Asteraceae to be the most important floral resource (e.g. Clausen et al. 2001, Wallisdevries et al. 2012) and therefore tested the following species or combinations of species for their potential in explaining abundance of flower-visiting insects: all flowers; *A. tripolium*; *A. tripolium* + *C. arvense*; all Asteraceae (*A. tripolium*, *C. arvense*, *Sonchus arvensis*, *Leontodon autumnalis*, *Tripleurospermum maritimum*), all non-Asteraceae.

Subsequently, we analyzed rotational grazing in comparison to continuous cattle grazing at high (1 cow ha^{-1}) and low (0.5 cow ha^{-1}) densities. First, we analyzed the total abundance over the three years, in a GLMM, with year and paddock nested in replicate as random factors. Secondly, because the rotational treatment was grazed in 2011 and 2013 and ungrazed in 2012, we looked at the yearly differences by analyzing the treatment effects for each year separately using GLMM with paddock nested in replicate as random factors.

RESULTS

Over the three year period, we observed 15 flowering plant species and counted 4,131 flower-visiting insects, of which 11 species of Lepidoptera. The floral resource base changed over the season and differed somewhat between years. In June of all years the floral resources were dominated by the prostrate species *Potentilla anserina* (33–70%) and *Glaux maritima* (29–65%), whereas in July *C. arvense* (15–45%) and *Spergularia* spp. (32–49%)

Table 6.1 Estimated relative abundance of the seven most abundant flowering plant species over all 15 500m transects per sampling period over the years 2011–2013 on a Dutch salt marsh.

	P. anserina	*G. maritima*	*C. arvense*	*Spergularia spp*	*T. maritimum*	*A. tripolium*
Preference by livestock*	-	-	--	-	-	++
June	33-70%	29-65%	0	<1%	<1%	0
July	0-38%	0-13%	15-45%	32-49%	0-11%	0-2%
late August	0-1%	-	<1%	0-5%	0-18%	77-100%

* according to Nolte (2014)

gained in abundance, with minor contributions by *P. anserina* and *G. maritima*. In August/September the marsh was dominated by the tall Asteraceae *A. tripolium* (77–100%) and *T. maritimum* (0–18%) (Table 6.1). All of these species were present in almost every paddock, whereas nine other species were mostly only present at one location in one or a few of the paddocks. The abundance of flower-visiting insects differed strongly between years, but was highest during the third observation round during all years (Table 6.2). Hoverflies accounted for 71% of all insects observed, followed by butterflies, accounting for 23%. Over the three years, the most abundant Lepidoptera species were the migratory *Aglais urticae* (336) and *Autographa gamma* (365) and the resident *Pieris rapae* (188). Several species, such as *Aglais io* and *Colias croceus* were only present in 2013 whereas *Thymelicus lineola* and honeybees (*Apis melifera*) were only observed in 2011 (Appendix 1).

Grazing treatments

There was a marginal effect of grazing treatments on total flower abundance ($\chi^2 = 2.08$, $p = 0.05$; Table 6.3), where floral abundance was lowest under high density horse grazing (Fig. 6.2A). When splitting flower abundance between Asteraceae and other flowers, we found that both density and species of livestock significantly explained abundance of Asteraceae. Highest abundances of Asteraceae were found under low density horse grazing, whereas lowest abundances were found under high density horse grazing (Table 6.3, Fig. 6.2A). Under cattle grazing the abundance of Asteraceae was intermediate, but did not differ significantly between low and high densities (Fig. 6.2A), nor was there a significant difference between horse and cattle grazing at the same density. Abundance of other flower species was only marginally affected by the treatments ($\chi^2 = 7.45$, $p = 0.06$)

There was a significant effect of grazing treatments on abundance of flower-visiting insects ($\chi^2 = 6.83$, $p = 0.008$). The only factor explaining abundance of flower-visiting insects remaining in the final model was stocking density, where flower visitors were more abundant at low density grazing than at high densities, but there was no difference between cattle and horses (Table 6.3, Fig. 6.2B).

Table 6.2 Total abundances of flower-visiting insects over 15 500 m transects over three sampling periods during 2011–2013 per round on a Dutch salt marsh. Flower visitors and flowers were counted by modified Pollard walks.

	2011	2012	2013
June	85	24	103
July	60	492	529
late August	184	1363	794
total	**329**	**1879**	**1426**

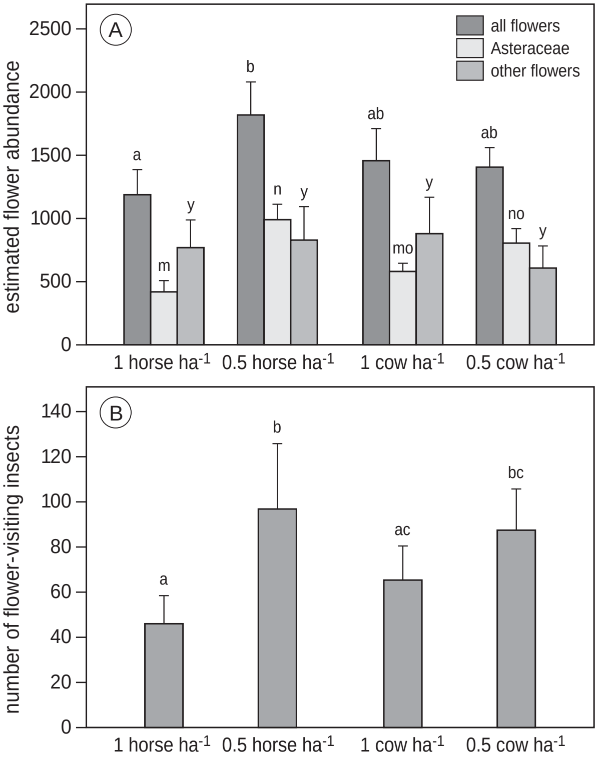

Figure 6.2 Mean abundance of floral resources (A) and flower-visiting insects (B) per 500 m transect under grazing by horses or cattle at 0.5 or 1 animal ha^{-1} installed in three replicates. Treatments denoted with the same letter (all flowers: a-c; Asteraceae n-o; non-Asteraceae: x-z) did not differ significantly at $p < 0.05$, according to GLMM and Tukey's HSD tests (see Table 6.2). Error bars denote standard errors.

Table 6.3 Summary statistics of the effects of livestock species (cattle or horses), density (0.5 or 1 animal ha^{-1}) and their interaction on the abundance of flowers and flower-visiting insects per 500 m transect in a triplicate grazing experiment on a salt marsh at the Dutch mainland Wadden-Sea coast. Measurements were taken three times yearly over three years, and assessed using GLMM. Flower abundance of each species was estimated in four classes and therefore represents the minimum number of flowers present. Z-values of the explanatory variables are only shown when the overall model is significant at $p < 0.05$.

	Livestock species		**Density**		**Species*density**		**Model**	
	z	p	z	p	z	p	chi^2	p
All flowers					-2.49	0.01	8.02	0.05
Asteraceae	2.79	0.006	-2.226	0.026	-3.00	0.003	16.49	**<0.001**
Other flowers							7.45	0.06
Flower-visiting insects			-3.2	0.001			6.83	**0.008**

Floral resources

There was a strong relationship between the abundance of flowers and of flower-visiting insects. Of all flower groups tested, the pooled Asteraceae reached the highest explanatory value ($F_{3,32} = 86.0$, $p < 0.001$, $R^2 = 0.89$; Table 6.4, Fig. 6.3A), whereas the abundance of other flowers was not related to the abundance of flower-vising insects ($p = 0.35$; Fig. 6.3B). The other tested groups all had significantly positive relations with the abundance of flower-visiting insects, but explanatory power was lower than for the pooled Asteraceae (Table 6.4). Year was a significant factor in all models, showing low values for 2011.

Exploration of rotational grazing

The full model comparing rotational grazing to continuous cattle grazing at low and high densities shows that over the three years, total flower abundance did not differ significantly between rotational and the continuous cattle-grazed treatments ($p = 0.36$; Table 6.5).

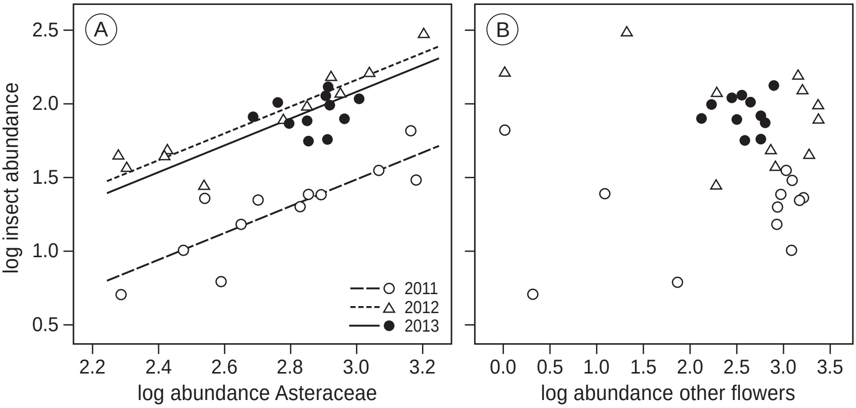

Figure 6.3 Relationship between abundance of flowers and flower visitors per 500 m transect (both log-transformed) over the four continous grazing treatments over 2011–2013 according to GLM (see Table 6.3). Only significant relations ($p < 0.05$) are shown.

Table 6.4 Relationships between the abundance of flowers and flower-visiting insects per transect (both log-transformed) over the four continuous grazing treatments over three years according to GLM. Year was a highly significant factor in all models (Fig. 6.2).

	Flower count		**Model**		
	t	p	F	p	R^2
All flowers	3.85	**<0.001**	$F_{3,32} = 28.02$	**<0.001**	0.72
A. tripolium	4.14	**<0.001**	$F_{3,32} = 29.93$	**<0.001**	0.74
A. tripolium and *C. arvense*	8.34	**<0.001**	$F_{3,32} = 73.34$	**<0.001**	0.87
All Asteraceae	9.22	**<0.001**	$F_{3,32} = 86.00$	**<0.001**	0.89
Other flowers	-0.95	0.35	$F_{3,32} = 16.51$	**<0.001**	0.61

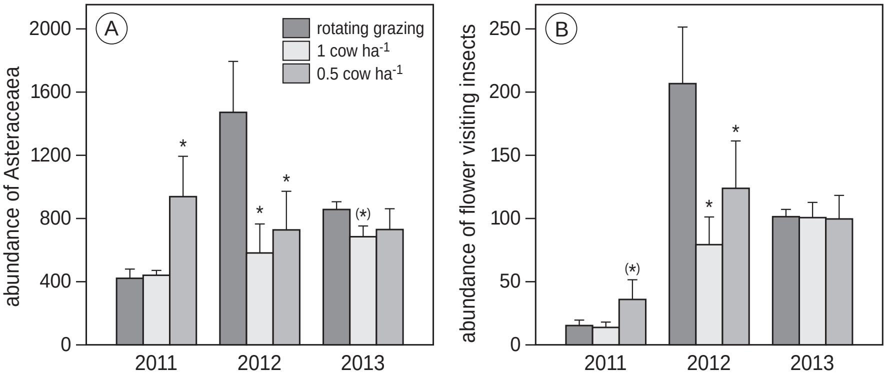

Figure 6.4 Effects of rotational grazing (yearly alternation of grazed and ungrazed) in comparison to continuous cattle grazing on the abundance of Asteraceae (A) and flower-visiting insects (B) over three years, where in 2012 the rotational paddocks were ungrazed. * Denotes significant difference from rotational grazing ($p < 0.05$), (*) denotes differences at $p < 0.1$.

Splitting flower abundance between Asteraceae and other species showed that Asteraceae were positively affected by rotational grazing (p = 0.006), while the other, mostly prostrate species showed only a marginally significant response, with lower abundance under extensive cattle grazing (p = 0.07; Table 6.5). Flower-visiting insects were significantly more abundant under rotational grazing than under the two continuously grazed treatments ($\chi^2 = 10.35$, p = 0.006; Table 6.5). When splitting between years, it became obvious that during the ungrazed years, the abundance of both Asteraceae and flower-visiting insects was significantly higher than the other treatments, whereas in the grazed years this was not the case (Fig. 6.4A,B).

Table 6.5 Summary statistics of the preliminary effects of rotational grazing treatment (alternated ungrazed and cattle grazed at 1 cow ha^{-1}) in comparison to continuous cattle grazing at 0.5 and 1 animal ha^{-1} on the abundance of flowers and flower-visiting insects per transect according to GLMM. Here, no difference was made between grazed an ungrazed years, as year was included as random factor.

	0.5 cow ha^{-1}		**1 cow ha^{-1}**		**Model**	
	z	p	z	p	chi^2	p
All flowers	-1.3	0.195	-1.39	0.166	2.02	0.36
Asteraceae	-1.98	0.05	-5.16	**<0.001**	10.26	**0.006**
Other flowers	-1.78	0.07	0.96	0.33	4.99	0.08
Flower-visiting insects	-2.65	**0.008**	-5.51	**<0.001**	10.35	**0.006**

DISCUSSION

We investigated the effect of different livestock species (horses and cattle) grazing at different densities and the effect of rotational grazing on the abundance of flowers and flower-visiting insects. As we had hypothesised, abundances of both flowers and flower-visiting insects were higher under low stocking densities (H1), and we found no significant difference between livestock species (H2). The abundance of high-quality floral resources in the form of tall Asteraceae species was found to be the main determinant for abundance of flower-visiting insects when corrected for year effects, as is in line with H3. Finally, we found preliminary evidence for the beneficial effects of rotational grazing on the abundance of flower-visiting insects (H4) in comparison to continuous cattle grazing at high or low densities.

Our results confirm the often reported negative relationship of abundance of flower-visiting insects with stocking density (Kruess and Tscharntke 2002b, Pöyry et al. 2004, Öckinger et al. 2006, Sjödin et al. 2008), where the rotational grazing yielded highest counts, especially in the ungrazed year. Although the positive effects of cessation of grazing have been shown on several occasions (Balmer and Erhardt 2000, Kruess and Tscharntke 2002b, Pöyry et al. 2004), the subsequent encroachment of tall grasses or shrubs is known to threaten the continued existence of characteristic grassland insect communities (Thomas et al. 1986, Balmer and Erhardt 2000, Öckinger et al. 2006). Rotational grazing therefore is an attractive alternative that could combine the positive effects of cessation of grazing with prevention of dominance of competitive tall species Although little explored, this management type was so far shown to be successful for insect conservation in calcareous grasslands (Morris et al. 2005) and production pastures (Farruggia et al. 2012, Scohier et al. 2013). Before sound conclusions can be drawn, more evidence is required to assess the long-term effects of this management type, especially whether it is able to prevent the dominance of the tall grass *E. artherica*, and to maintain high abundances of *A. tripolium* over a large number of years.

We did not detect a difference between cattle and horse grazing. Previous work on the experimental setup presented here, showed that horses exert more trampling damage than cattle (Mandema et al. 2013), which had a negative effect on the most important flower species *A. tripolium*, especially under high densities (Nolte et al. 2013). Selective defoliation of *A. tripolium*, however, was more severe under low density cattle grazing than low density horse grazing, and the total abundance of flowering *A. tripolium* was therefore highest under low density horse grazing (Nolte et al. 2013).

The importance of tall Asteraceae species, and most notably *A. tripolium* for flower-visiting insects was evident, and it is likely that herbivorous insects will also benefit from any type of management that allows this plant to reach high flower densities. *Aster tripolium* is one of the few entomophilous plant species typical for salt-marsh habitats (Meyer et al. 1995) and has a rich herbivorous fauna, consisting, among others, of several specialised species of flies, aphids and moths. It is, however, also preferred forage for livestock (Kiehl et al. 1996, Nolte et al. 2013), and flowering individuals become increasingly rare with an increase in stocking density of sheep (Kiehl et al. 1996) or cattle and horses (Nolte et al. 2013).

Generally, herbivorous insects reach highest diversity and abundances on tall, well-developed host plants (Morris 1967, Lawton 1983, Völkl et al. 1993, Tscharntke 1997, Gómez and González-Megías 2007) which was confirmed by measurements on *A. tripolium* in the same experimental setup presented here (box I). Furthermore, on German salt marshes it was shown that sheep grazing is highly detrimental to the moth species living on *A. tripolium*, where under moderate to high sheep densities (4–10 sheep ha^{-1}) these species had largely disappeared (Rickert 2011, Rickert et al. 2012).

A general pattern emerging here is that whether flower visitors and herbivorous insects benefit from grazing or not, depends on the palatability of their preferred food plant for livestock. Palatable plant species and their associated insect fauna can suffer from herbivory by mammals even at moderate stocking densities, if such plant species are selected for (Kiehl et al. 1996, Vulliamy et al. 2006, Yoshihara et al. 2008). Unpalatable plant species and their fauna may benefit from grazing at moderate stocking densities, as these are selected against by large herbivores (chapter 4). Under high stocking densities, some grazing-tolerant and unpalatable plant species may provide food for a rich pollinator community (Vulliamy et al. 2006) but this management type is generally detrimental to herbivorous insects (chapter 2). Under ungrazed conditions, rich communities of both insect herbivores and pollinators are often found (Kruess and Tscharntke 2002b, Pöyry et al. 2004, Vulliamy et al. 2006), but flowering plants risk disappearing as a consequence of being outcompeted by tall species after long-term abandonment (Grime 1973).

Management recommendations

Our results, although still preliminary regarding the effects of rotational grazing, clearly show that for the conservation of flower-visiting insects on salt marshes, the best opportunities develop at grazing with 0.5 animal ha^{-1} or rotational grazing. These grazing treatments showed higher densities of both Asteraceae flowers and flower-visiting insects, and it is likely that also the herbivorous fauna of these plant species will benefit. The high predictive value of the flower abundance of Asteraceae indicate that yearly counts of Asteraceae flowers may be a cost-effective option for monitoring foraging opportunities for flower-visiting insects, although total abundance of flower visitors will differ between years.

ACKNOWLEDGEMENTS

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Box I

The herbivorous fauna of *Aster tripolium* on grazed and ungrazed salt marshes

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INTRODUCTION

To understand the effects of grassland management on arthropod communities, it is important to understand the mechanisms by which these communities are affected (chapter 2). For specialist herbivorous insects, characteristics of the host plant strongly determine their development, and defoliation by large herbivores can cause large changes in the morphology and chemistry of this host plant (Morris 1967, Ydenberg and Prins 1981, Nolte et al. 2013). Additionally, grazing can cause changes in microclimate and the relative abundance of host plants (chapter 2). These factors may affect the abundance and species richness of herbivorous insects on their host plants in grazed grasslands.

On the salt marshes of the Wadden Sea, grazing management is common practice for purposes of nature conservation or coastal protection (Esselink et al. 2009). How this affects herbivorous insects on the level of individual plants and how this interacts with the surrounding habitat is, however, unclear. The aim of this investigation was, therefore, to understand the factors affecting the fauna of the common halophyte *Aster tripolium* on grazed and ungrazed salt marshes.

Aster tripolium (Asteraceae), hereafter referred to by its generic name, is a biennial halophyte native to both the higher and lower salt marsh and can reach up to 150 cm height (Weeda 1999). The species is very palatable for livestock (Kiehl et al. 1996, Nolte et al. 2013) and has a rich fauna of specialised and polyphagous insect herbivores (Tischler et al. 1994).

METHODS

We collected 60 individuals of *Aster* in three of the treatments of the grazing experiment at Noord Friesland Buitendijks (for details see chapter 6) during the main flowering period (September 2010): Cattle-grazed marsh (1 cow ha^{-1}), the one-year ungrazed marsh of the rotational grazing treatment and in the long-term ungrazed marsh in the western replicate (see also chapter 5) stratified over the high marsh and the low marsh (10 plants each, in each paddock). The plants were enclosed in a plastic bag and transported to the lab. At the location of each plant, we recorded height of the vegetation surrounding the plant using a drop-disk, and we estimated how many *Aster* individuals were present in a 25 m radius around the plant by counting the number of plants along two 25 m transects, north and south of each sampled plant. Along both transects, we counted the number of individuals per square metre. Along the first five metres we counted in each square metre, but from 5 m onwards every second square metre. Thus, we counted the total number of individuals in 30 square metres of surrounding vegetation of each sampled plant.

In the lab, all ectophagous and stem-boring insects were carefully collected from the sampled plants and identified to species level, genus (some caterpillars) or morphospecies (aphids). We checked 20 randomly chosen flower heads per plant for flower dwelling insects because it was impossible to check all (often several hundreds) flower heads per plant. We extrapolated this number to the total number of flower heads. Additionally, we measured the height of the plant, counted flower heads and weighed the plant after drying for 48 hours at 70°C. All collected insects known not to feed on *Aster* were omitted from analyses.

Statistical analysis

We used generalised linear models to assess the relationship between the grazing treatments and salt-marsh zone on insect abundance, richness, plant biomass, number of *Aster* individuals and surrounding vegetation height. Secondly, we used these proximate variables (plant biomass, surrounding vegetation height and number of conspecifics in a 25 m radius) to construct a model of the ecological variables affecting the abundance and species richness of herbivores on flowering individuals of *Aster*. In case of a significant interaction between grazing regime and marsh zone, we split that dataset for the low and high marsh and performed the analysis for each zone separately. Models were accounted for over-dispersion of the variance by using the quasipoisson function. All statistical analyses were done in R3.0.1. For each grazing treatment we calculated species accumulation curves based on the number of individuals using BiodiversityR package.

RESULTS

In total we collected 1.062 insects from 60 plants, belonging to 16 (morpho-) species (Table B1.1). The number of flower-dwelling insects was extrapolated to account for the total number of flowers per plant. There was a strong positive correlation between plant biomass, and number of flower heads (r = 0.87), and a moderately strong positive correlation between plant height and biomass (r = 0.64), therefore we will use biomass as proxy for these attributes in the remainder of the text. There was also a strong positive correlation between number of insect individuals and number of species per plant (log transformed) (Fig. B1.1).

The grazing treatments had a significant effect on the attributes of *Aster*, the surrounding vegetation, and the number of herbivorous insects living on the plants (Table B1.2). There was a significant interaction between marsh zone and grazing treatment for all plant and environmental variables, but not for insect abundance or species richness (Table B1.2). Plant weight was highest on the high zone of the one-year ungrazed marsh and lowest on the lower grazed marsh, but plants were tallest at the low marsh of the long-term ungrazed treatment. The number of *Aster* plants and the height of the surrounding vegetation were highest in the lower zone of the long-term ungrazed marsh and lowest on the higher grazed marsh (Table B1.2). Insects were significantly more abundant and included more species in the one-year ungrazed marsh than in the other treatments, which did not differ from each other (Table B1.2; Fig. B1.2).

The individual-based species accumulation curves show a parallel increase for the grazed and the one-year ungrazed marsh, although the curve of the grazed marsh terminates earlier. A slightly lower slope is visible for the long-term ungrazed marsh (Fig. B1.3).

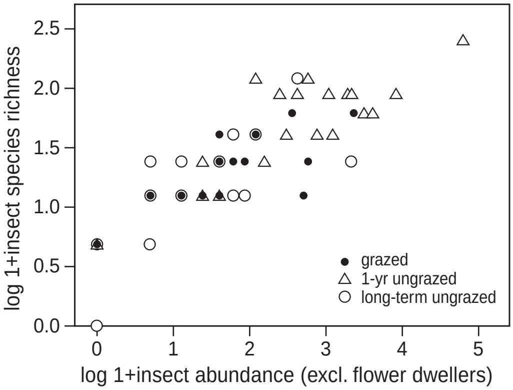

Figure B1.1 Relation between number of insect individuals (excluding flower dwellers) and number of species per plant (both log transformed).

Table B1.1 Species and morpho-species of herbivorous insects found on 60 Aster individuals on grazed and ungrazed salt marshes at the Dutch mainland coast.

	Number of individuals
Lepidoptera	
Coleophora asteris	2
Eupithecia spec.	1
Heliothis spec.	1
Phalonidia affinitana	22
Bucculatrix maritima (mines)	43
*Eucosma tripoliana / rubescana***	68 *
Coleoptera	
Longitarsus reichei	3
Diptera	
Campiglossa plantaginis	3178 *
Agromizidae mine	254
Hemiptera-Heteroptera	
Closterotomus norvegicus	1
Hemiptera – Aphidoidea	
Aphid 1	95
Aphid 2	41
Aphid 3	9
Aphid 4	3
Aphid 5	4
Aphid 6	3

* Extrapolated from the counts in 20 flowers per plant
** Two flower mining species that are indistinguishable at the larval stage

Table B1.2 Effects of grazing treatment and salt-marsh zone on the weight of *Aster*, the surrounding vegetation, and the number of insect herbivores found per plant. When the interaction between grazing treatment and salt marsh zone was significant ($p < 0.05$), the data were analysed separately per zone. For the different grazing treatments, the average (±se) of the untransformed data is given. Different letters denote significant differences between treatments (per zone) according to post-hoc Tukey tests.

	model type		grazed β(±se)	1-yr ungrazed β(±se)	long-term ungrazed β(±se)	zone		inter-action		Model	
						z	p	z	p	χ^2	p
plant weight	GLM (Log transformed)	high marsh	5.8(±1.0)^A	20.2(±3.4)^B	9.61(±2.8)^A				*	7.28	**0.001**
		low marsh	3.3(±0.8)^A	11.4(±2.7)^B	16.1(±4.3)^B				*	12.39	**<0.001**
plant height	GLM (Log transformed)	high marsh	40.6(±2.4)^A	64.6(±4.5)^B	78.9(±4.2)^C				*	2.32	**<0.001**
		low marsh	29.5(±1.9)^A	52.6(±3.9)^B	86.7(±4.4)^C				*	1.19	**<0.001**
height surrounding vegetation	GLM (Log transformed)	high marsh	11.9(±0.9)^A	15.9(±1.2)^B	24.7(±1.8)^C				*	2.73	**<0.001**
		low marsh	11.1(±0.9)^A	20.6(±1.5)^B	36.9(±4.1)^C				*	6.69	**<0.001**
A. tripolium in 25 m radius	GLM Quasipoisson	high marsh	1.3(±0.3)^A	0.8(±0.1)^A	3.0(±1.0)^B				*	14.38	**<0.001**
		low marsh	3.7(±0.4)^A	9.0(±0.9)^B	13.0(±1.6)^C				*	54.13	**<0.001**
insect abundance	GLM Quasipoisson		6.0(±1.5)^A	22.3(±5.9)^B	4.4(±1.5)^A		ns		ns	325.54	**<0.001**
insect species richness	GLM Poisson		2.6(±0.4)^A	4.9(±0.7)^B	2.6(±0.5)^A		ns		ns	18.17	**<0.001**

*significant interaction

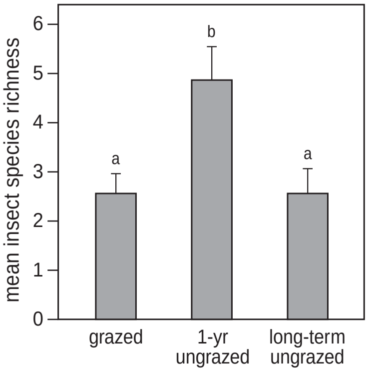

Figure B1.2 Effects of grazing treatments on insect species richness per individual plant. The effect of marsh zone was not significant.

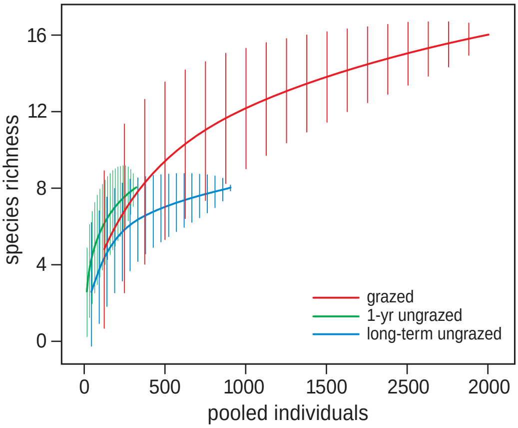

Figure B1.3 Accumulation curve for insect species richness based on total number of individuals for three grazing treatments. The slopes of the grazed and one-year ungrazed are similar, but the slope of the long-term ungrazed marsh seems to deviate.

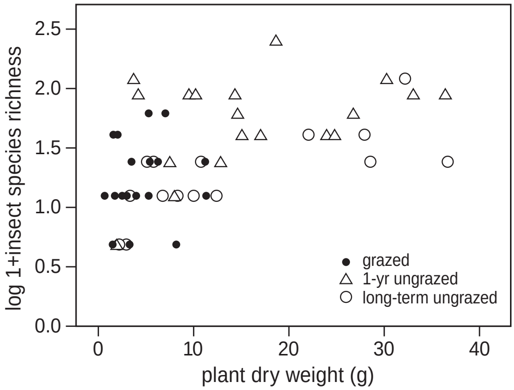

Figure B1.4 Relation between plant biomass and insect species richness for different treatments.

Extrapolation suggests that if the curve of the grazed marsh were to be extended, at least seven times as many individuals of *Aster* are required to harbour the same number of insect species as on the one-year ungrazed marsh, whereas in the long-term ungrazed marsh this number may never be attained (Fig. B1.3).

When considering the variables ecologically relevant to the insects, total abundance of herbivorous insects per plant, (excluding flower-dwelling species) was explained only by plant dry weight ($t = 3.2$, $p = 0.003$). None of the other variables (grazing, number of *Aster* plants, or surrounding vegetation height, nor any of the interactions between these variables) had a significant effect. Some caution is needed here, however, since the clumped occurrence of especially aphids caused a large spread in the residuals. Insect species richness had a positive relation with plant dry weight ($z = 5.12$, $p < 0.001$; Fig. B1.4) and number of conspecifics in a 25 m radius ($z = 2.96$, $p < 0.003$), while height of the surrounding vegetation had a negative effect ($z = -3.39$, $p < 0.001$). Interactions between these variables were not significant.

DISCUSSION

The lines of evidence presented here suggest that plant size is the most important determinant of the number of species occurring per individual of *Aster*, but also the number of conspecifics in surrounding vegetation and vegetation height play a role. The heavier plants can support more insect individuals, corresponding with more species. This agrees with previous research showing larger and structurally more complex plant species (Tallamy and Denno 1979, Lawton 1983, Reid and Hochuli 2007) and individuals within a species (Morris 1967, 1971), to support more herbivorous, and also carnivorous insects (Luff 1966, Reid and Hochuli 2007) than smaller plants.

Grazing by large herbivores had a negative impact on the number of insect individuals and species per *Aster* plant. This is in line with previous research on the insects on other plant species in grassland systems (Morris 1967, 1971, Völkl et al. 1993, Gómez and González-Megías 2002, Rothenwöhrer et al. 2013). However, there seems to be an additional factor of influence in the long-term ungrazed marsh. Here, the number of insect species was as low as in the grazed marsh, although the plants were taller and heavier than even in the 1-year ungrazed marsh. There were also higher numbers of *Aster* plants in the vicinity, but the surrounding vegetation was taller. Still, the species accumulation curves suggest a different relationship between number of individuals and species than in the other treatments. Several factors may explain this result. First, it is possible that the tall surrounding vegetation caused a colder microclimate, unfavourable to insects, on the individual plants during the growing season, leading to a lower number of individuals and therefore fewer species on these plants. Secondly, the height of the surrounding vegetation, and the dense packing of *Aster* individuals may have driven the plants to grow taller, but carrying fewer flowers. This may have caused the plants to be less structurally complex, or to have a higher C/N ratio, both of which may be negative to the insects living on a plant (Lawton 1983, White 1993). Finally, there may be negative effects of the higher sedimentation rates in the long-term ungrazed marsh (S. Nolte unpublished data). The insects living on *Aster* develop relatively late in the season (August-September) and therefore, most hibernate as larva or pupa. High sedimentation loads may cause large numbers of these insects to be buried and failing to emerge in summer, which will decrease population sizes, and therefore the number of species per plant. Possibly, each of these explanations contributes in determining the lower number of insects on the plants in the long-term ungrazed marsh. It is unclear, however, to what extent this pattern is general, and replication of the study would be needed before extrapolating this result to salt-marsh management.

Although not measured, there were no indications that changes in plant chemistry after defoliation by large herbivores play a role in determining the abundance or richness of insect herbivores. The chemistry of *Aster* is not well known, but its high palatability to both insects and vertebrate herbivores suggests that secondary compounds are unimportant as anti-herbivory strategy. The effects of defoliation by large herbivores on plant chemistry and on the community of herbivorous insects may be better studied on plant species with a well-known plant-chemistry, such as *Brassica oleracea* (Poelman et al. 2008).

CONCLUSIONS

We have shown here the highly beneficial effects of short-term cessation of grazing on the herbivorous fauna of *Aster*. It seems that one year of cessation is sufficient to increase the populations of these species, but this is not the case for all plant species. In inland grasslands, the stem borers of the grass *Dactylis glomerata* were shown to require at least two years of grazing exclusion in order to increase in population size (Rothenwöhrer et al. 2013).

In most cases the complete cessation of grazing on salt marshes, is undesirable for the conservation of the herbivores of *Aster*, because of the known encroachment by tall grasses and decrease of plant species richness (Bakker et al. 2003). When grazing is resumed, stocking densities should be applied that allow sufficient numbers of plant individuals and their herbivores to survive. Grazing with cattle or horses at 0.5 animal ha^{-1} or less seems adequate for this purpose (see also Nolte et al. 2013, chapter 6), but grazing by the highly selective sheep is already detrimental to the flower production of *Aster* at moderate stocking densities (Kiehl et al. 1996), and has strong negative effects on the moths feeding on it (Rickert 2011). The present research, therefore, suggests that rotational grazing with yearly rotations is a promising management option for insect friendly salt-marsh management. Its long-term success in preventing the dominance of tall grass species (especially *Elytrigia atherica*), should, however, be investigated thoroughly.

ACKNOWLEDGEMENTS

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Box II

Contrasting effects of microclimate and defoliation on the fauna of five halophytes

Roel van Klink, Jan P. Bakker, Michiel F. WallisDeVries

INTRODUCTION

Grazing and browsing by ungulates causes physical and chemical changes in the defoliated plants and can result in changes in its direct environment. This can have large impacts on the specialised herbivorous insects living on these plants. Some of the most important factors determining host-plant quality for herbivorous insects are plant biomass (Morris 1967, 1971, Bailey and Whitham 2006) and microclimate (Thomas et al. 1986, Roy and Thomas 2003, Eilers et al. 2013). In order to study by which of these mechanisms large grazers affect herbivorous insects on salt marshes, we set up a full-factorial manipulation experiment of defoliation and shading on five common halophytes (in order of declining plant height): the forbs *Aster tripolium*, *Artemisia maritima* and *Plantago maritima*, and the grasses *Festuca rubra* and *Puccinellia maritima* (hereafter referred to by their generic names). Plants were greenhouse grown and placed in the field to be colonised by their herbivorous insects over the growing season.

For tall-statured host plants it is well known that plant biomass, and hence structural complexity, is one of the most important factors determining the number of insect individuals and species that can live on a plant (Morris 1967, 1971, Tallamy and Denno 1979, Lawton 1983, Tscharntke 1997). We therefore expected that for the tall forbs *Aster* and *Artemisia*, defoliation is the most important factor determining herbivore load.

Microclimate, on the other hand has been shown to be important to butterfly species living on short-statured host plants, and many species are confined to warm microclimates, even on common host plants (Thomas 1983, Thomas et al. 1986, Roy and Thomas 2003). Cessation of grazing was shown to cause a cooler microclimate due to rapid growth of the surrounding vegetation, negatively affecting the development of these species. Therefore, we expect the fauna of the short-statured plants *Plantago*, *Puccinellia* and *Festuca*, to be negatively affected by shading.

METHODS

The experiment was conducted on the salt marsh of Noord Friesland Buitendijks (Fig. 1.2), in a fenced area in the grazed marsh (elevation 45cm +MHT). All of the investigated plant species are common on this marsh and were present at <100 m from the experimental plots. At the start of the experiment (May 2011), all vegetation was short (< 5 cm) from grazing by large flocks of winter-staging geese (Mandema 2014).

Studied plant species

Aster tripolium (Asteraceae) is a biennial halophyte native to both the high and low salt marsh and can reach up to 150 cm height (Weeda 1999). The species is very palatable for livestock (Kiehl et al. 1996, Nolte et al. 2013) and has a rich fauna of both specialist and generalist insect herbivores (Tischler et al. 1994, box I, box III).

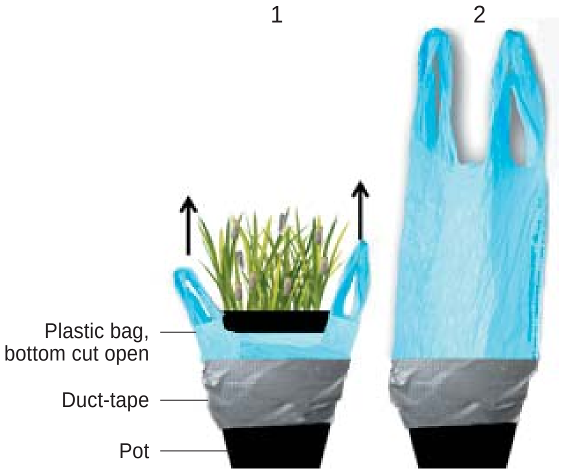

Figure B2.1 Method for catching ectophagous insects on short-statured potted plants. A plastic bag with cut open bottom encloses the pot before plants are colonised by insects. The handles of the bag stick out above the pot and the soil surface, while the rest of the bag is hidden beneath the edge of the pot (1). When the handles are pulled up, the bag unfolds (2), trapping the insects.

Artemisia maritima (Asteracae) is an aromatic perennial halophyte native to the higher salt marsh. It can grow up to 60 cm tall and is generally unpreferred by livestock (Nolte 2014), probably due to high concentrations of alkaloid secondary metabolites (Weeda 1999). The species has a rich fauna of specialised (mono- or oligophagous) herbivorous insects (box III), but polyphagous species are rarely encountered on it (Tischler et al. 1994). It flowers not before the second year after establishment.

Plantago maritima (Plantaginaceae) is a perennial halophyte occurring on both higher and lower salt marshes (Weeda 1999). It is highly palatable to livestock (Nolte 2014) and geese (Ydenberg and Prins 1981) and has a rich fauna of specialised insect herbivores (See box III).

Puccinellia maritima (Poaceae) is the dominant grass species of lower salt marshes and is host to a range of specialist as well as generalist insects (see box III). It is also preferred food for both livestock and geese.

Festuca rubra ssp *litoralis* (Poaceae) is the dominant grass species of the middle and higher marsh of most Wadden Sea salt marshes (Beeftink 1977). No salt-marsh specific insects are known to be specialised on this plant species, but most species feeding on *Puccinellia* also feed on *Festuca*. It also heavily grazed by livestock and geese.

Experimental design

We set up a full-factorial experiment of manipulation of host plant size by clipping (0, 1 or 2 times over the growing season) and manipulation of the microclimate of the host plant by clipping or not clipping of the surrounding vegetation (monthly) (n = 10 per treatment level). The plants were arranged randomly in eight plots that were separated by a 50 cm strip undisturbed vegetation. The vegetation of four of the plots was clipped monthly to a height of 5 cm; the vegetation in the other plots was left to grow uninhibited. Clipping was done to a height of 5 cm for the grass species, 8 cm for *Plantago* and 10 cm for *Aster* and *Artemisia*. Due to high mortality of *Aster* at the start of the experiment, only sufficient sample size remained for one clipping treatment and the unclipped control. Clipping took place on June 15th for the clipped once treatment and on June 15th and July 15th for the clipped twice treatment.

Origin and pre-treatment of experimental plants

All plants except *Aster tripolium* were kept in the greenhouse in pots with soil consisting of 1/3 standard garden soil, 1/3 sand and 1/3 salt-marsh clay collected from the field site from March until May 2011. The experimental plants were obtained from wild populations in several ways: Seeds of *Artemisia* and *Festuca* were collected in 2010 and sown in the greenhouse. Of F*estuca*, 50 seeds were sown in each Ø10cm pot. *Artemisia* plants were sown in a large container on March 8th and each plant was transplanted into a separate pot on April 22nd. P*uccinellia* was collected as roots from the field in March 2011, since not enough viable seeds had been obtained the previous year. Ten grams (fresh weight) of washed roots were spread throughout each pot. All plants were watered daily and, to accustom them to the saline conditions of the salt marsh, received saline water (salinity of the Wadden Sea) once per two weeks. The plants from the greenhouse were transferred into the field and placed in 10 cm deep holes in the salt-marsh surface in May 2011. Of the biennial *Aster* we collected root stocks with rosette leaves from the field site on the 20th of May. These were washed, weighed and directly transferred to Ø15 cm pots with the same soil mixture as the other plants.

Data collection

The grasses and *Plantago* were harvested between August 20th and 29th 2011. One month prior to harvest, each pot was equipped with a plastic bag which was cut open at the bottom and attached to the pots using duct tape (Fig. B2.1). The two handles of the bags stuck out above the pot, so that when pulled, the plastic bag would envelop the experimental plant, trapping all insects on it. *Aster* was harvested during it main flower period, on September 15th 2011, and *Artemisia* was harvested one year later, on August 28th 2012, so that plants could reach maturity. These tall forbs were harvested by enclosing them in plastic bags and pulling them from the soil. All bags containing plants and insects were taken to the lab, where all insects were collected. *Aster* plants were also checked for species living in the stem and flower heads, and for traces of leaf mining species as described in box II. Above ground biomass of all plants was weighed after drying at 70°C for 48 hours. All insects were stored in 70% alcohol and later identified to species level, except for aphids, which were assigned to morpho-species.

Statistics

We used generalised linear models (GLM) to assess how plant dry weight and herbivore abundance were affected by clipping (numerical variable) and shading (factorial) at the time of harvest. Logarithmic or square root transformations were applied to plant dry weight in order to correct heteroscedacity. Effects on insect abundance were tested using Poisson distributed models, where necessary corrected for overdispersion, using the quasi-poisson functionality. All analyses were done using R.3.0.2 (R Core Team 2013).

RESULTS

We found 718 herbivorous insects on 266 surviving plants. The most common species was the halophilic leafhopper *Macrosteles sordidipennis*, which feeds on *Puccinellia* and to a lesser extent on *Festuca* (Table B2.1). On Aster the most common species was the flower-

Table B2.1 Herbivorous insects found on four halophytes in a manipulative experiment of shading and clipping.

	Aster	*Artemisia*	*Puccinellia*	*Festuca*
n =	44	52	58	59
Lepidoptera				
Coleophora asteris	1			
Phalonidia affinitana	7			
Eucosma tripoliana / rubescana	6			
caterpillar spec.			1	
Coleoptera				
Longitarsus reichei	1			
Cassida vittata			1	
Diptera				
Campiglossa plantaginis	127			
Stem mining diptera	2			
Agromizidae mine	4			
Hemiptera-Heteroptera				
Europiella decolor		5		
Hemiptera - Auchenorrhyncha				
Eupteryx artemisiae		1		
Streptanus sordidus			1	
Macrosteles sordidipennis			318	171
Psammotettix putoni			6	5
Javesella pelucida				1
Hemiptera - Aphidoidea				
Aster aphid 1	9			
Grass aphid 1				2
Grass aphid 2			3	
Artemisia aphid 1		38		
Artemisia aphid 2		8		
number of individuals	**157**	**52**	**330**	**179**
number of species	**8**	**4**	**6**	**4**

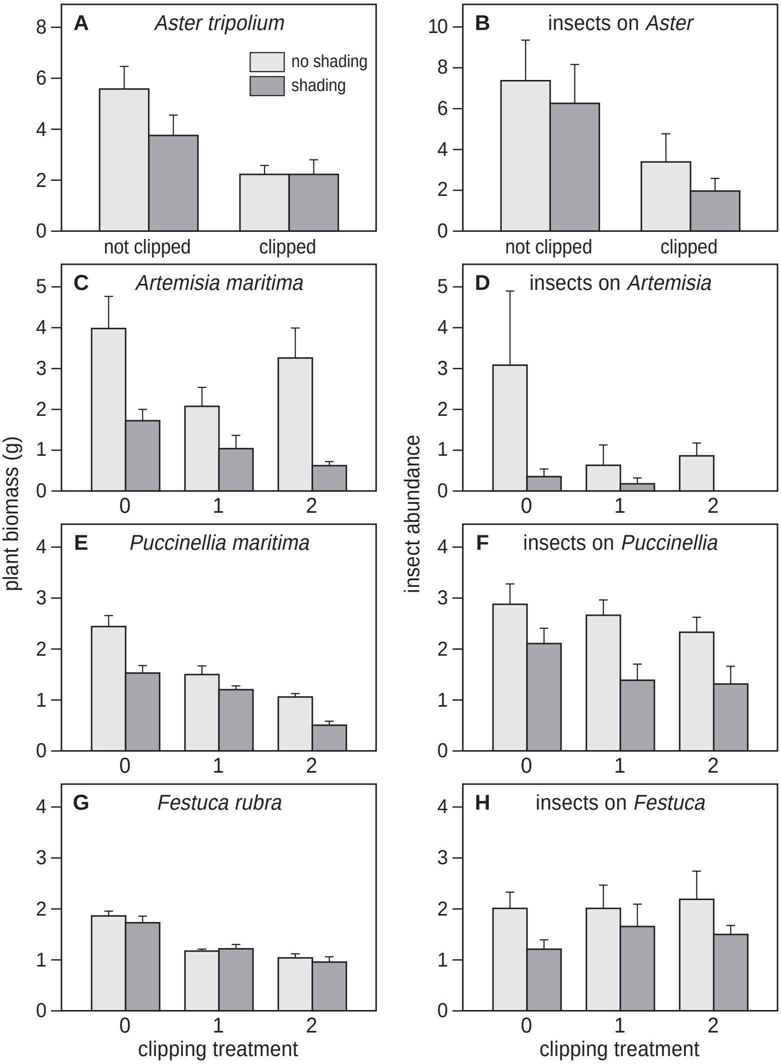

Figure B2.2 Responses of plant dry weight and insect abundance per individual plant of four halophytes to shading and defoliation by clipping. Shading was provided by letting the vegetation surrounding the experimental plants grow and clipping was done zero, one or two times over a 3.5 month period.

dwelling fruit fly *Campiglossa plantaginis*, and on *Artemisia* an unidentified aphid species. On *Plantago* no herbivores known to feed on it were found, and therefore this species will not be further analysed.

Of *Aster*, almost one third of all plants were lost to drought after replanting their rootstocks, and therefore only one clipping round was administered. Defoliation by clipping was the only significant driver of plant biomass (Table B2.2, Fig. B2.2A). Herbivore load was determined solely by the clipping treatment (Table B2.3, Fig. B2.2B).

Biomass of *Artemisia* was, after two years of growth, primarily negatively affected by shading, with a minor role for defoliation (Table B2.2, Fig.B2.2C). The only significant factor explaining herbivore load was shading.

Regarding the grasses, of *Puccinellia*, biomass was decreased by both defoliation and shading, while biomass of *Festuca* was only significantly reduced by defoliation (Table B2.2, Fig. B2.2E,G). Herbivore load of both species, however, was only negatively affected by shading, but not by defoliation, although for *Festuca* this effect was only marginally significant (Table B2.3; Fig. B2.2F,H).

Table B2.2 Effects of clipping and shading on plant dry weight.

	Model type	**Clipping**		**Shading**		**Interaction**		**Model**	
		t	p	t	p	t	p	χ^2	p
*Aster **	GLM (sqrt transformed)	-4.2	**<0.001**		ns		ns	4.52	**<0.001**
Artemisia	GLM (log transformed	-2.15	**0.04**	-4.17	**<0.001**		ns	12.61	**<0.001**
Puccinellia	GLM (sqrt transformed)	-11.32	**<0.001**	-6.7	**<0.001**		ns	3.83	**<0.001**
Festuca	GLM (untransformed)	-9.81	**<0.001**		ns		ns	6.6	**<0.001**

* start weight was included in models but was not significant

Table B2.3 Effects of treatments on herbivore abundance per individual plant.

	Model type	**Clipping**		**Shading**		**Interaction**		**Model**	
		t	p	t	p	t	p	χ^2	p
Aster	GLM Quasipoisson	2.66	**0.011**		ns		ns	39.62	**0.007**
Artemisia	GLM Quasipoisson		ns	-1.91	0.06		ns	33.76	**0.01**
Puccinellia	GLM Poisson		ns	-2.61	**0.009**		ns	7.06	**0.007**
Festuca	GLM Poisson		ns	-1.814	0.07		ns	3.36	0.07

DISCUSSION

In this experiment we evaluated host-plant suitability based on the abundance of herbivorous insects per plant. For this we relied on colonisation of greenhouse-grown plants by wild insects over a three-month period (plus one year for *Artemisia*). There were large differences in colonisation success between insect species. The mobile grass-feeding leafhopper species that abound at the site appeared not to be limited in colonisation, and also for the *Aster* inhabiting species were abundant on the experimental plants. However, our experimental *Aster* individuals were smaller than their wild conspecifics, and insect load per individual plant was also much lower in comparison to box I. This may have been caused by the drought the plants experienced after potting, or the generally poor weather in 2011. In the case of Plantago, however, three months seem to have been too short to allow colonisation of the experimental plants, despite high abundances of this species and the occurrence of at least two monophagous weevils and a leafbeetle at the site. The *Artemisia* plants, stayed in the field an additional year, as it was important that this plant could reach maturity. Still, colonisation appeared to be limited, despite the extra time, with several species that are abundant elsewhere on this and other salt marshes (Rickert 2011, chapter 4, pers obs) reaching only low abundances, and other species being absent.

For the plants that harboured insects, we found contrasting drivers of herbivore load on the different plant species. While biomass of all plant species was reduced by clipping, the abundance of herbivorous insects was only negatively affected by this treatment on *Aster*. This agrees with previous findings where the fauna of *Aster* was found to proliferate on large, undamaged host plants and was increasingly negatively affected with increasing stocking densities (Irmler and Heydemann 1986, Rickert 2011, chapter 4, box I).

The herbivores living on *Artemisia* were only negatively affected by shading. However, biomass was strongly confounded with the shading treatment, hence, the low insect abundance could also have been caused by low plant biomass. Indeed, in chapter 4 (Table 4.2) we showed that for the monophagous herbivores of *Artemisia*, abundance correlated well with host plant cover, suggesting an important role for plant biomass. These were, however, all well-established mature plants, and in the current experiment we only worked with young plants, most of which were very small and only few individuals were able to grow taller than the surrounding canopy height within two years. Therefore it seems that during establishment *Artemisia* suffers severely from light competition, but mature plants are relatively resilient to competition with tall grasses and reach high cover percentages during the first years after cessation of grazing (Bakker 1978) and under moderate stocking densities (chapter 4). We, tentatively conclude that plant biomass is the primary driver of herbivore load on *Artemisia*, and that this is more likely to be affected by shading by other plants than by defoliation by ungulates, since this plant species is highly unpalatable.

For the grasses *Puccinellia* and *Festuca*, our hypothesis that shading would be the main determinant of insect abundance was supported, although the effects on *Festuca* were only marginally significant. Biomass of *Festuca* was not affected by shading, explaining its general resilience to competition with the dominant grass *Elytrigia atherica* up to 20 years after cessation of grazing (chapter 4). The ectophagous insects living on these grasses were unaffected by defoliation, but responded negatively to shading, suggesting negative effects of cessation of grazing on these species.

These findings generally agree with results from German salt marshes in the 1980s (Irmler and Heydemann 1985). They found the halophilic leafhopper *Psammotettix putoni* to increase in population size during the first year after cessation of grazing, as long as grass was growing fast, where after population sizes declined rapidly. Another halophilic species, *Macrosteles sordidipennis*, the most common species in our experiment, was found to reach highest densities under intermediate stocking densities (Irmler and Heydemann 1985), agreeing with our results and additional observations (Fig. 8.2).

However, not all ectophagous grass feeding species are known to respond positively to grazing. Especially the inland leafhopper species *Streptanus sordidus* as well as the halophilic species *Aphrodes aestuarina* and *Anoscopus limicola* and the moth *Whittleia retiella*, which all live deep in the vegetation, benefitted from cessation of grazing (Irmler and Heydemann 1985, Rickert 2011, chapter 4). This shows that, while species feeding on *Aster* and *Artemisia* all seem to benefit from high plant biomass, grass feeding species have strongly differing preferences. This is in agreement with Table 4.2, where grass feeding species showed very poor correlations with cover percentage of their host plants.

Conclusion

We showed strong differences in response of the fauna of different halophytes to defoliation and shading, but did not investigate changes in plant chemistry. Plant chemistry is known to be of high importance to herbivorous insects, due to differences in concentrations of carbon, nitrogen, defensive compounds (reviewed by Awmack and Leather 2002), and in the case of halophytes also salinity (Bethge 1973, Hemminga and Van Soelen 1988, 1992). Because currently next to nothing is known about especially the defensive chemistry of halophytes, we focused only on defoliation and microclimate, but it would be interesting to investigate their cascading and interacting effects on plant chemistry and herbivore load, as was done for some woody plant species (e.g. Martinsen et al. 1998, Riipi et al. 2005). Currently, however, most knowledge on community-wide effects of plant chemistry on herbivorous insects is derived from greenhouse experiments on a limited set of plant species (e.g. Poelman et al. 2008), and these may be better suited for this purpose than wild halophytes.

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Chapter 7

Foraging site choice and diet selection of Meadow Pipits *Anthus pratensis* breeding on grazed salt marshes

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Joost M. Tinbergen

*These authors contributed equally to this work

ABSTRACT

Capsule Breeding Meadow Pipits foraged for caterpillars and large spiders in vegetation that was less heterogeneous than vegetation at random locations.

Aims To gain a better understanding of the foraging ecology of breeding Meadow Pipits on grazed coastal salt marshes, we tested three hypotheses: 1) there is a positive relation between vegetation height and prey abundance, 2) adult birds would preferentially forage at locations with great heterogeneity in vegetation height, thereby maximising both food abundance and accessibility, and 3) adult birds will forage selectively for specific prey items.

Methods We measured food availability in relation to vegetation structure, habitat use and nestling diet for six individual nests. Nestling diet was determined by microscopic analysis of faeces while food availability over different vegetation heights was estimated by suction sampling. Information on habitat use was gathered by direct observation. Foraging locations were compared to random locations at the same distance from the nest.

Results Nestling diet mainly consisted of larger spiders (>5 mm) (38% of prey individuals), caterpillars (ca. 2 cm) (38%), other insect larvae (12%) and flies and wasps (7%). There was a positive relation between vegetation height and prey availability. Contrary to our expectations, vegetation at Pipit foraging locations was less heterogeneous than at random locations, yet we found no evidence for a preference for short or tall vegetation. We found strong evidence for selective foraging for larger prey, since the relative abundance of especially large spiders and caterpillars was much higher in the faecal samples than in the field. This diet differed considerably from Meadow Pipit diet reported from other habitats.

Conclusion These findings suggest that the creation of heterogeneity in vegetation height by grazing or otherwise may not be invariably beneficial to breeding Meadow Pipits.

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INTRODUCTION

Meadow Pipits (*Anthus pratensis*) are common grassland birds in the Netherlands with relatively stable breeding population since 1990 (Boele et al. 2013). They form an important food source for red-listed Harrier species (*Circus cyaneus*, *C. pyrargus*, *C. aeruginosus*) (Redpath 1992, Koks et al. 2007), and have been suggested to be good bio-indicators of habitat quality for grassland birds (Vanhinsberg & Chamberlain 2001). Many populations of Meadow Pipits and other grassland birds all over Europe are threatened by agricultural intensification (Benton et al. 2002), but populations of inaccessible and unproductive grasslands are at risk of agricultural abandonment (Suárez-Seoane et al. 2002).

On the coastal salt marshes of Western Europe, Meadow Pipits are also a common breeding bird, but changes in management may affect these populations. Historically, most salt marshes in Western Europe were grazed with livestock. During the past decades, however, extensive livestock grazing has become no longer economically feasible, leading to either intensification of grazing or abandonment (Bakker et al. 1993, Bouchard et al. 2003). Abandonment of salt marshes quickly leads to a homogeneous tall vegetation structure and the dominance of the tall Sea Couch Grass (*Elytrigia atherica*) (Bakker et al. 1993). This tall and dense vegetation is unfavourable to many ground-breeding bird species, as it impedes movement of foraging adults and chicks and decreases accessibility of prey, (Milsom et al. 2000, Vickery et al. 2001). In other grassland types, abandonment has indeed been shown to cause a decline for several bird species (Suárez-Seoane et al. 2002; Sirami et al. 2008). The recent changes in grazing management of salt marshes may therefore pose a threat to Meadow Pipits and other grassland birds, but little is known about their habitat requirements in this grassland type. The purpose of this study, therefore, was to gain a better understanding of the foraging ecology of breeding Meadow Pipits on salt marshes, particularly in relation to food availability and vegetation structure.

Previous studies on foraging passerines on inland grasslands generally suggest a trade-off between the accessibility and the abundance of food items (e.g. Fuller & Gough 1999; Atkinson et al. 2004; Butler & Gillings 2004; Devereux et al. 2004). Birds that hunt visually for ground-dwelling invertebrates, such as Meadow Pipits, can easily manoeuvre through short vegetation. Moreover, prey detectability in short vegetation is greater (Butler and Gillings 2004). Yet, the abundance of most invertebrate groups, including important food sources for Meadow Pipits is greater in tall vegetation (e.g. Luff 1966, Dennis et al. 2008). Heterogeneous grasslands, combining tall vegetation with patches of bare ground and short vegetation, are therefore likely to provide the greatest food availability for Meadow Pipits and other grassland birds (Vickery et al. 2001, Atkinson et al. 2005, Evans et al. 2006). Livestock grazing at low densities can increase the structural vegetation heterogeneity (Adler et al. 2001), and may therefore be an adequate management option for optimising availability and accessibility of food for Meadow Pipits and other typical grassland birds, such as Skylark (*Alauda arvensis*), Redshank (*Tringa totanus*), Lapwing (*Vanellus vanellus*) and Starling (*Sturnus vulgaris*) (Norris et al. 1997, Devereux et al. 2004, Evans et al. 2006, Vandenberghe et al. 2009).

The diet of Meadow Pipits known from inland populations mainly consists of flies (Diptera), beetles (Coleoptera), spiders (Araneae), bugs (Hemiptera), wasps (Hymenoptera) and moth larvae (Lepidoptera) (reviewed by Wilson et al. 1996), though diet differs between different habitats (Walton 1979; Douglas et al. 2008; Hågvar et al. 2011). Meadow Pipits were shown to select the larger species and individuals of the available prey as food for their chicks (Hågvar et al. 2011). For salt-marsh breeding populations, diet is currently unknown, and might differ from inland populations due to the habitat specific fauna of salt marshes. The invertebrate fauna of grazed salt marshes is dominated by spiders and beetles, as well as springtails, flies and leafhoppers (Irmler and Heydemann 1986, Ford et al. 2013). In tall, ungrazed salt-marsh vegetation, however, abundance and biomass of invertebrates is higher than on grazed salt marshes with short vegetation (Ford et al. 2013). This is mostly attributable to the high abundance of larger spiders (Pétillon et al. 2007), and the semi-terrestrial crustacean *Orchestia gammarellus* (Ford et al. 2013).

We hypothesize that 1) prey availability shows a positive relation with vegetation height, 2) breeding Meadow Pipits on salt marshes will select foraging locations that have a greater number of transitions from tall to short vegetation than random locations, exploiting the enhanced accessibility of prey at the interface of tall and short vegetation, and 3) the diet of Meadow Pipit nestlings on salt marshes reflects the locally available prey, but we also expect selective foraging for larger items.

METHODS

Study site

This study was conducted on a mainland salt marsh at the Dutch Wadden Sea Coast (53° 20′ N, 5° 44′ E). The salt marsh was developed by promoting sedimentation with construction of sedimentation fields and a rigid ditch structure (every 10 m) during the early 20th century (Verhoeven 1980, Esselink et al. 2009). Although the study area has a history of agriculture, it is now managed as nature reserve. Cattle grazing, with a stocking density of 1 animal ha^{-1}, has been employed over at least ten years preceding this investigation aiming to maintain high levels of plant diversity and retard succession to plant-species poor, tall vegetation. The area is important for a number of breeding wader and passerine species, and for foraging raptors and short-eared owls (*Asio flammeus*).

Diet composition of Meadow Pipit nestlings

To determine the diet composition of Meadow Pipit nestlings, we collected faecal samples of nestlings found over 2009 – 2011. Nestlings (age 4–7 days) were handled briefly, which would generally result in a dropping being produced. If no droppings were produced within ten minutes, no faecal samples were collected from the nest. Faecal samples were stored in 70% ethanol until identification.

We identified all parts of invertebrates present in a faecal sample to the highest taxonomic level possible. This was often class or order level for the very fragmented remains of adult insects, whereas spiders could generally be identified to species level, based on their genitalia (using a private reference collection from the same area, identified using Roberts (1987)), but were later grouped as large (body length >5 mm) or small (<5 mm). Parts of most invertebrate groups were well preserved. The relative abundance of spiders, caterpillars and flies are approximated well by faecal samples, while beetle abundance is generally overestimated according to a comparison of neck collars of nestlings and faecal analyses of three passerine species (Moreby and Stoate 2000). All of these invertebrate taxa have hard parts that are well preserved (Ralph et al. 1985). Soft bodied taxa, like springtails, however may be underestimated using this method (Moreby and Stoate 2000).

For every sample (one dropping) we determined the minimum number of prey items of each (group of) species by matching the parts found. We assumed that unidentifiable parts belonged to an individual of which other parts were identified. Individual invertebrates possess two or more of many parts (e.g. jaws, legs, wings or pedipalps (male genitalia of spiders)), hence if matching left- and right-hand parts were present, we assumed these to belong to the same individual. Therefore, the numbers counted should be seen as the minimum number of individual invertebrates eaten.

Parts of spider legs were omitted from the counts because they were often numerous and not attributable to any number of individuals. Unless no other spider parts were present in the sample we assumed that leg-parts belonged to already counted individuals. Jaws of insect larvae and spiders were matched based on size, saw pattern and coloration. The size of the caterpillars was estimated based on the size of the jaw parts by M.G.M. Jansen using a private collection. Species or groups present in the faeces (>2%) were designated 'actual prey'.

Vegetation height and prey abundance

We tested whether there was a positive relation between vegetation height and invertebrate abundance by sampling invertebrates at locations independent of Meadow Pipit nests over the complete range of vegetation heights present at the site. We did this in a stratified random sampling design, taking samples at six locations with short vegetation (<10 cm), six locations with vegetation of intermediate height (10–20 cm) and six locations with tall vegetation (>20 cm) (for details on the sampling protocol see below). Intermediate and tall vegetation types together accounted for 24% of the area, according to a vegetation map (S. Nolte, unpublished data).

Foraging observations

To determine where adult Meadow Pipits forage during the breeding season, we adapted the method of Douglas et al. (2008) and Vandenberghe et al. (2009). Observation towers (height 3 m) were erected at the centre of the study site to provide a good view over the entire salt marsh used by Meadow Pipits. Nests were located by visual observations of adult Meadow Pipits carrying food and by flushing incubating females. The exact locations of the nests were recorded in a handheld GPS (accuracy ca. 3m) and marked on a map. In this way we located 15 nests during the period 6 May and 6 June, of which five were predated, two abandoned, and two fledged before observations could be conducted, leaving a total of six nests. At each of these nests, three one-hour observations were conducted during dry weather and the first observation round started when the chicks were 3–5 days old. Observations were only carried out early mornings (between 6:00 and 10:00) on consecutive days (weather permitting). Observations were done from the observation towers, or in case of nests that were >50 m from the tower, observations were conducted from a mobile tower erected at 50 m from the nest. The observations were always conducted by the same team of three people.

The observation rounds were started when a Meadow Pipit was seen leaving its nest. All locations where Pipits were observed to forage were drawn onto a map, which allowed high accuracy due to the ditch structure typical for mainland salt marshes. The most frequently visited foraging location (generally two times as often as the other locations) of each observation round was later visited for sampling vegetation height, vegetation heterogeneity and prey abundance.

The distance from a nest to each of the three foraging locations was determined using a measuring tape when the nestlings had fledged (maximum one week after determining foraging locations). At the same distance from the nest, but in a random direction, a paired random location was established for comparisons of vegetation parameters and availability of food for Meadow Pipit nestlings. The direction was randomised by throwing a wooden stick straight up and using the direction indicated by the stick once on the ground.

Sampling protocol

At all locations (foraging locations n = 18), random locations (n = 18), and the independent locations measured for the range of vegetation height (n = 18, see Table 7.1) we sampled vegetation parameters and invertebrates following a standardised sampling protocol: At each location (from here onwards called a 'square' *sensu* Vandenberghe et al. (2009)), we set up a grid of 6 m × 6 m (9 grid cells of 2 m × 2 m) using string. We sampled invertebrates in all four corners of the central grid cell. As a measure of vegetation heterogeneity, we recorded the number of transitions between short and tall vegetation along the four central 6m strings (as defined by Bakker et al. (1984): tall vegetation >10 cm, with a distinct litter layer, short vegetation <10 cm, no litter layer).

At each of the four corners of the central area we first estimated vegetation height by lowering a Ø25 cm, 75 g Styrofoam drop disk onto the vegetation along a calibrated stick (Holmes 1974), and applied suction sampling for invertebrates. Suction sampling was done using an inverted leaf blower (Echo Shred 'n' Vac, Ø15 cm, maximum air velocity 73 ms^{-1}) equipped with a 1mm mesh net. Because tall vegetation is well known to inhibit efficient suction sampling (Brook et al. 2008), we used a two-stage suction protocol. First we applied suction to the vegetation layer in a Ø50 cm sampling ring for 30 seconds, after which we clipped all biomass from the ring and applied suction to the litter layer for another 30 seconds (see van Klink et al. 2013). In this way we sampled (4 × 0.196 m^2 =) ca. 0.75 m^2 per square. All invertebrates were collected and identified in the field by manually sorting the contents of the net to the same taxonomic groupings revealed by faecal analysis. The groups collected could therefore be classified as 'actual prey' (species also present in faecal samples) or 'potential prey' (all invertebrates present in the field).

Statistical analyses

All statistical tests were conducted with R.15.3 (R Core Team 2013). We tested for differences in the number of individuals between groups in the faecal samples using Poisson-distributed generalised linear mixed models (GLMM) from the lme4 R-package (Bates et al. 2012). We used 'sample' nested in 'nest' as random factors, prey number as dependent, and prey group as explanatory variable. Similarly, differences in the frequency of occurrence of the different groups over the samples (proportion of samples in which a prey group was present) were tested by binomial GLMM with 'sample' nested in 'nest' as random factors.

We assessed the relationships between mean vegetation height and invertebrate abundance per square using Poisson-distributed general linear models (GLM) for the following invertebrate groups: all invertebrates combined (potential prey), all actual prey and the most abundant actual prey groups. Additionally, we calculated the proportion of all invertebrates that belonged to the groups designated as 'actual prey'. The relation between this proportion and vegetation height was tested using binomial GLM.

Differences in prey abundance, vegetation height, and vegetation heterogeneity between the observed foraging squares and paired random squares were assessed using GLMM, with the pairs of random- and foraging squares within nest treated as nested random variables. Differences in vegetation height were log-transformed before analysis, and differences in vegetation heterogeneity (number of transitions between short and tall vegetation) and prey abundance (actual prey) were assessed with Poisson-distributed models. The relation between relative abundance of the different prey groups in the faecal samples and at the foraging and random squares was assessed for all invertebrate groups making up more than 2% in either the faeces or the field (97% of the individuals). We tested for significance using Mann-Whitney U-tests. An overview of sample sizes and statistical tests used for the different aspects of the study can be found in Table 7.1.

Table 7.1 Summary of sample sizes and statistical models used for different parts of the study.

	N nests	N Samples	Years	Statistical test
Faecal samples	13	23	2009–2011	GLMM
Gradient of vegetation height	-	18	2011	GLM
Foraging / random locations	6	36 (18 / 18)	2011	GLMM
Relative abundance in faeces and field measurements	-	23/36		Mann-Whitney U

RESULTS

Diet composition

We obtained 23 faecal samples from 13 nests over the period 2009-2011. From eight nests only one sample was obtained, from the other five nests two to four samples were collected after observation rounds, produced by one ad-hoc selected chick in the nest. From these samples we identified 214 prey individuals, 38% of which were spiders and another 38% caterpillars (Lepidoptera). Other prey classes were less abundant: other insect larvae (mostly larvae of soldier beetles (Cantharidae)) made up 12% of the diet, flies and wasps 7%, molluscs 3% and beetles less than 2%. On a sample basis, there were significant differences between these groups (GLMM: $\chi^2 = 89.2$ $p < 0.001$, Fig. 7.1A). Spiders and caterpillars were equally abundant, but were significantly more abundant than any of the other groups, while beetles were least abundant (Fig. 7.1A). Spider parts were present in every sample we analysed and all but one of the individuals belonged to species >5 mm body length (according to Roberts (1987)). The most abundant remains were of the halophilic wolf spider *Pardosa purbeckensis*, the most common larger spider occurring on

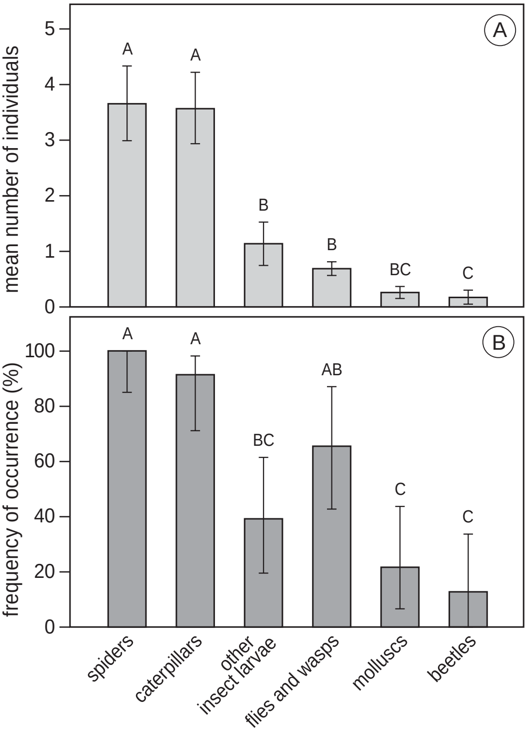

Figure 7.1 Diet composition of Meadow Pipit nestlings based on 23 faecal samples from 13 different nests, collected 2009–2011 at a mainland salt marsh at the Dutch Wadden Sea coast. A) mean number of invertebrate individuals per sample (mean ±se), B) frequency of occurrence of the different invertebrate groups over all samples (% ± 95% CI). Different letters denote significant differences ($p < 0.05$).

salt marshes (Ford et al. 2013). The smallest species found in the faeces was *Pachygnatha degeeri*, which has a body length of ca. 4 mm, and was found only once. The caterpillars were, based on the size of the jaws (ca. 0.425 mm) approximately 2 cm in length (M.G.M. Jansen pers. comm.), and were present in over 90% of the samples. Remains of insect adults (flies (Diptera) and (parasitic) wasps (Hymenoptera)) were present in 65% of the samples, but always in low numbers (Fig. 7.1A,B). Molluscs, both bivalves and gastropods, were also found in several samples. Beetle remains were found in three samples and belonged to smaller species, although a definite identification could not be made.

Relation of prey abundance and vegetation height

Mean vegetation height at the independent squares ranged from 5 to 46 cm, with 21 to 101 invertebrate individuals per sampled square (in total 1087 individuals). Based on the faecal analysis we consider the following arthropod groups to be actual prey for Meadow Pipit nestlings: spiders (body size >5 mm) (*Pardosa purbeckensis*, *Enoplognatha mordax*, *Clubiona stagnatilis*, *Pachygnatha clercki*, *Stemonyphantes lineatus* and *Trochosa ruricola*), caterpillars (body size ca. 2 cm), other insect larvae, flies and wasps, pupae, and molluscs. All other groups found (small spiders, beetles, cicadellid leafhoppers, spittlebugs, true bugs, adult soldier beetles and ladybirds) were not considered to be important prey items, as they were very rare or not present in the faecal samples.

There was a strong relationship between vegetation height and abundance of actual prey (GLM: $\chi^2 = 28.3$, $p < 0.001$), but no relationship between total invertebrate abundance (potential prey) and vegetation height (GLM: $\chi^2 = 0.3$, $p = 0.58$, Fig. 7.2A). Of the main food items only spiders and caterpillars were abundant enough to allow statistical inference. Spider abundance showed a positive relation with vegetation height (GLM: $\chi^2 = 183.9$, $p < 0.001$, Fig. 7.2B), but caterpillar numbers were not related to vegetation height (GLM: $\chi^2 = 0.1$, $p = 0.75$). There was a significant positive linear relationship between percentage of actual prey items (actual prey/potential prey) and vegetation height (GLM: $\chi^2 = 35.4$, $p = 0.001$; Fig. 7.2C).

Foraging locations

Foraging observations yielded a total of 116 foraging locations, on average 6.4 (range 4–18) per observation session. The maximum foraging distance observed was 208 m, but 76% of all foraging locations were closer than 75 m from the nest (median 46 m).

There was no significant difference in vegetation height between the foraging and random squares (GLMM: $\chi^2 = 0.69$, $p = 0.4$). Vegetation height ranged 4–14 cm, with a median value of 5.5 cm. There was also no significant difference between the foraging squares and the paired random squares in abundance of actual prey (median = 8 individuals; GLMM: $\chi^2 = 2.3$, $p = 0.13$). Vegetation heterogeneity, based on the number of transitions between tall and short vegetation, was significantly lower at the foraging squares than at the random squares (GLMM: $\chi^2 = 20.1$, $p < 0.001$. At the foraging squares the number of transitions ranged 0–20, with a median value of 9, whereas at the random squares the number of transitions ranged 4–38, with a median value of 13.

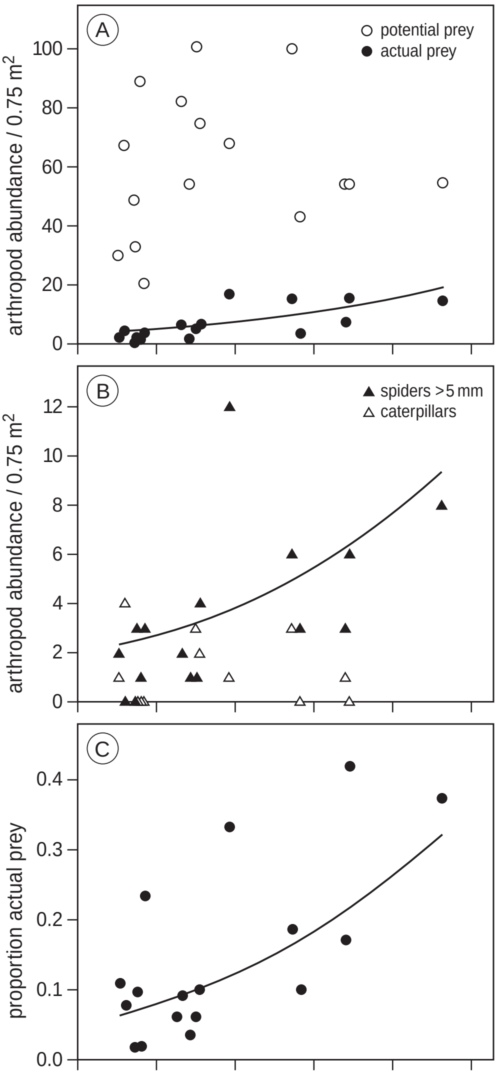

Figure 7.2 Relationships between vegetation height and invertebrate abundance. A) abundance of potential prey (all invertebrates in the vegetation) and actual prey (invertebrate groups also present in the faecal samples), B) abundance of the most important actual prey groups (large spiders (body length >5 mm) and caterpillars (ca. 2 cm)), C) percentage actual prey items of all invertebrates. Fitted curves according to glm are only shown for significant relationships.

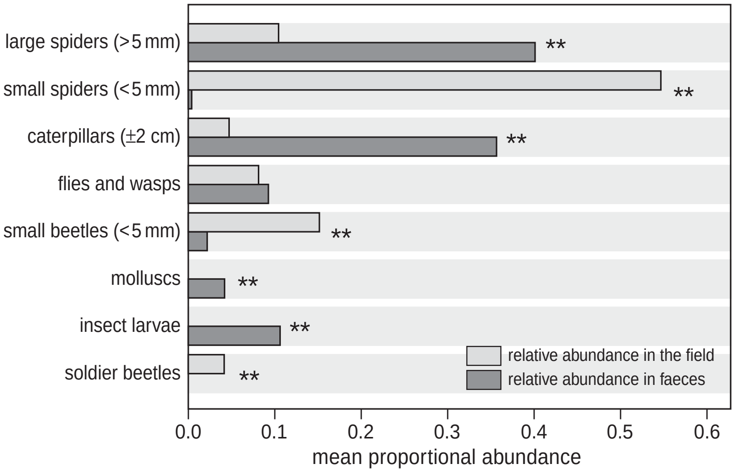

Figure 7.3 Difference in relative abundance of all invertebrate groups present in faecal samples (n = 23) and in field samples (n = 36). Groups making up less than 2% of both pools were omitted. *p < 0.05, **p < 0.001 according to Mann-Whitney U tests.

Comparing the relative abundance of the different invertebrate groups found in the faecal samples and in the field revealed strong selective foraging by Meadow Pipits (Fig. 7.3). Large spider species (>5 mm), caterpillars (ca. 2 cm), molluscs and other insect larvae were more often found in faeces than would have been expected based on their relative abundance in the field. Conversely, small spiders (< 5 mm) and beetles (<5 mm), as well as the larger soldier beetles were rare in faecal samples, but were abundant in the field. Only flies and wasps were as abundant in the field as in the diet (Fig. 7.3).

DISCUSSION

Our field measurements confirmed the positive relation between vegetation height and abundance of invertebrate prey (e.g. Luff 1966, Dennis et al. 2008) but we did not find a preference for foraging in short vegetation, as was found in other habitats (Douglas et al. 2008; Vandenberghe et al. 2009). Furthermore, contrary to our expectations, we found that Meadow pipits to forage preferentially in less heterogeneous vegetation. This contradicts the suggestion that heterogeneity in vegetation height is an important characteristic of Meadow Pipit foraging-habitat (Vickery et al. 2001, Atkinson et al. 2005). We did find strong evidence for selectivity of Meadow Pipits in prey choice.

In our measurements, both the foraging squares and the random squares exhibited some heterogeneity in vegetation height, but the number of transitions between tall and short vegetation was lower at foraging squares. We therefore conclude that Meadow Pipits on salt marshes had a preference for foraging in relatively homogeneous vegetation. Fine grained vegetation mosaics, characterised by a large number of transitions between short and tall vegetation, appear to be unattractive to foraging Meadow Pipits. Possibly highly heterogeneous vegetation impairs overview of the foraging location and visibility of predators. Whatever the reason, our results suggest that, if a too fine-grained mosaic of short and tall stands develops, grazing may decrease preferred foraging habitat for Meadow Pipits.

We did not find a difference in mean vegetation height of the foraging and the random squares. Previous studies have shown varying preferences of Meadow Pipits regarding their foraging habitat. Some studies have found this species to preferably forage in short vegetation (Douglas et al. 2008, Vandenberghe et al. 2009), while other studies report Meadow Pipits to be generally associated with taller vegetation (Vanhinsbergh and Chamberlain 2001, Atkinson et al. 2005). Such an ambiguous relation was also reported regarding Meadow Pipit's winter habitat (Atkinson et al. 2004). Our results may indicate that Meadow Pipits do not have a clear preference for vegetation of a specific height at their foraging locations, but alternatively within foraging range, large areas with vegetation of the preferred height may have been available, hence, we did not detect a difference between foraging and random sites. Nevertheless, these locations differed in horizontal vegetation heterogeneity, i.e. the number of transitions between tall and short vegetation, and our results therefore suggest that the horizontal heterogeneity might better describe Meadow Pipit foraging habitat than vegetation height.

Diet composition of nestling Meadow Pipits breeding on salt marshes differed from compositions reported from other habitats. We found a dominance of spiders and caterpillars, whereas in the Scottish uplands, leatherjackets (Tipulidae larvae) were reported to comprise 70% of the nestling diet(Evans et al. 2005). Apart from Tipulidae larvae and adults, spiders and Lepidoptera larvae were also selected more than their relative abundance predicted, in this habitat (Douglas et al. 2008). Conversely, in mountainous areas of Wales, diet of nestling Meadow Pipits mainly consisted of adult Diptera and larvae of both Lepidoptera and saw flies, whereas spiders were absent (Walton 1979). In the alpine tundra of Norway, tipulid adults were also found to form a large part of the diet, combined with Plecoptera and insect pupae (Hågvar et al. 2011). Furthermore, the importance of rove beetles (Staphylinidae) in the diet of Meadow Pipits (Wilson et al. 1996) was not supported by our findings, despite the high abundance of this beetle family at our study area (R. van Klink unpublished data). Meadow Pipit diet clearly varies among habitats probably in part because these birds adjust their diet to the locally available food.

We found strong evidence for selectivity in prey choice. The diet of nestlings was highly consistent over the faecal samples we analysed and matched with species present on salt marshes (Irmler and Heydemann 1986, Ford et al. 2013, van Klink et al. 2013). However, large groups of invertebrates that are extremely abundant in this habitat were not found in the faeces, most notably small spider species (<5 mm) (mostly of the family Linyphiidae) and small beetle species (of the genera *Ochtebius, Helophorus* and *Bembidion*). Beetle and spider parts are generally well preserved (Ralph et al. 1985), and if the smaller species had been part of the diet, their remains should have been apparent in our samples. Moreover, in a study comparing diet estimated with neck-collars on the chicks with faecal analysis (Moreby and Stoate 2000), it was found that with faecal analysis the abundance of beetles in bird diets is rather overestimated than underestimated. This strongly suggests that these species are selected against by Meadow Pipits. The energetic costs of catching and providing these small invertebrates to nestlings may outweigh the energetic gain for nestlings (Kacelnik 1984, Wright et al. 1998). Conversely, remains of Collembola and other soft bodied taxa are rarely found in bird faeces, as large proportions of these animals are digested (Moreby and Stoate 2000). Therefore, these species may have been missed in our analysis. The mollusc shells found in the faeces may have had a role as gastroliths rather than as actual prey. This may indicate that mollusc shells are of importance for Meadow Pipits on salt marshes, since small stones, as found in the stomachs of both adult and nestling Meadow Pipits by Hågvar et al. (2011) are scarce in the heavy salt marsh clay.

Our study does not allow a comparison between differently managed salt marshes, but our measurements show that Meadow Pipits do not always select the most heterogeneous vegetation available for foraging. Livestock grazing at intermediate densities on salt marshes can create considerable vegetation heterogeneity (Berg et al. 1997) which can be favourable for Redshank and Oystercatcher (Norris et al. 1997, Mandema et al. in press). Intensive livestock grazing (>1 livestock units (LU) ha^{-1}) on salt marshes is likely to be detrimental to Meadow Pipits and other grassland birds, as it decreases the abundance of their most important food sources: large spiders (Meyer and Reinke 1996) and caterpillars (Rickert et al. 2012). Moreover, risk of trampling nests increases with increasing stocking density, and is higher under horse grazing than under cattle grazing (Mandema et al. 2013). Stocking densities ranging 0.5 – 1 LU ha^{-1} therefore seem an adequate management option. Salt marshes have a high plant production as a result of input of sediment during inundations. Less productive grasslands will be stronger affected by similar stocking densities.

In other grassland types, research on the impact of livestock grazing on Meadow Pipit densities has produced varying results. In the Scottish uplands, higher Pipit densities were found under moderate, mixed sheep/cattle grazing than under either high or moderate density sheep grazing or cessation of grazing (Evans et al. 2006). In the in the Norwegian mountains, however, higher densities were found under high stocking densities than under low densities or no grazing (Loe et al. 2007). This indicates that for bird conservation optimal management may differ over ecosystems. Extrapolation of results from other habitats is therefore risky. In order to understand these contrasting results between grassland types, a more mechanistic understanding is needed of the effects of different species of grazers at different densities in different grassland types. Only then can we understand how changes in management affect populations of breeding birds and their prey.

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Box III

Combining faunistic and ecological knowledge to optimise conservation management for salt-marsh invertebrates

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In prepraration for publication

INTRODUCTION AND METHODS

We compiled a list of arthropod species in north-western Europe (United Kingdom, Ireland, Denmark, Germany, Netherlands, Belgium and France north of Brittany) confined to salt marshes, based on literature, expert judgement and entomological collections, in order to synthesize the knowledge on species-specific responses of arthropods to management. The list is restricted to the species occurring only in the coastal and inland salt marshes, and excludes other coastal habitats, such as coastal dunes, beaches and rocky shores.

We defined species or sub-species as endemic to the North Sea basin based on known distributions, with the North Sea basin extending west to Ireland, south to the English Channel and east to the western part of the Baltic Sea. Red list status for the Wadden Sea area is based on Von Nordheim (1996) and is only available for molluscs, spiders and beetles.

We used the data collected for this thesis and published literature to determine the response of each species to grazing management. We distinguished four levels of grazing: high stocking density (1 horse / 1.5 cow /10 sheep ha^{-1}), intermediate stocking density (0.5 horse/ 4 sheep/ 1 cow ha^{-1}), low stocking density (1-3 sheep/ 0.5 cow ha^{-1}) and cessation of grazing: (with or without dominance of *Elytrigia atherica*). Furthermore, for the herbivores of *Aster tripolium* and *Artemisia maritima*, we assumed a similar response to grazing as in other specialists of these plants, since according to chapter 4 and box I and II there was a good correlation between insect abundance and host plant cover/ biomass.

DISCUSSION

For less than half of the 173 invertebrate species in this list, the response to grazing management has been studied, or can be extrapolated with reasonable certainty. This has two possible reasons: 1) the species occur outside the marsh zones where management is commonly applied, living at the edge of creeks or the seaward marsh edge, between or on pioneer plants such as *Spartina anglica* or *Salicornia* ssp., or 2) these species are rare or difficult to assess, for example the ground beetle *Acupalpus elegans* or the moths *Aristotelia brizella* and *Lobesia littoralis*, the latter two feeding on *Armeria maritima*. Although the host is not uncommon, these moth species were rarely found (Rickert 2011).

The species for which the response to management has been assessed, show high variability in their response, with 27 species reaching highest densities under moderate to high stocking densities and 38 species reaching highest densities under ungrazed conditions or low stocking densities, or even dominance by *E. atherica*. This suggests that the highest chances of conservation success for all of these species can be achieved when several types of grazing management and abandonment are conducted in close proximity, effectively creating a large-scale mosaic of vegetation types.

A number of general rules regarding the management effects on different groups of arthropods can be deduced from this overview, which can help making management decisions for salt marshes:

1. **Species occurring only in the pioneer zone** of salt marshes (ca. 13 species), such as the ground beetle *Pogonus luridipennis*, the springtail *Axelsonia littoralis* and species feeding on pioneer plants such as *Salicornia* spp. and *Spartina* spp. **should be little affected by grazing management**, at least, if grazing is applied at low to intermediate densities. Typically, large grazers will not enter the pioneer zone, and a gradient of increasing vegetation height from the fresh water source to the sea has been observed (Kiehl et al. 1996, Nolte 2014). It is unlikely that grazing management on higher parts of the marsh can create conditions that are favourable for these species. They may, however, be vulnerable to erosion at the seaward side of salt marshes
2. **Herbivorous insects living on tall plants** (> 20 species) **perform best when host plant biomass is high**. *A. tripolium*, which is palatable to livestock, generally attains highest plant biomass in the absence of grazing (Box I, Box II). For plant species unpalatable for livestock, such as *Art. maritima*, highest abundances often occur under moderate grazing densities (chapter 4). On more sandy marshes, the spiny *J. maritimus* also reaches high densities under moderate grazing (see the salt marsh of Schiermonnikoog). This can possibly benefit its herbivorous fauna, but quantitative data are unavailable. The smaller rush *J. gerardii* seems also to be avoided by smaller herbivores such as sheep (chapter 4) and geese (personal observation), but is readily consumed by cattle and horses (Bakker et al. 2008). Therefore, specialist herbivores of *J. gerardii* may well benefit from sheep grazing (chapter 4) but not from cattle grazing.
3. **Short statured forbs and their specialised fauna** such as *Arm. maritima, Pl. maritima* and *G. maritima* (> 14 species) are prone to disappear within a few years after cessation of grazing, as a result of competition with tall species, most notably *E. atherica*. Specialist herbivores living on these plants are therefore dependent on grazing for sustenance of their host plants, but not all of these herbivores have been shown to benefit from grazing management. Especially the moth species living on these plants were not found in high numbers on salt marshes studied by Rickert (2011), despite the high abundances of the host plant. For species feeding on *Arm. maritima* this may be partially explained by their overwintering strategy in the flower heads of the host plant, but for *Scrobipalpa samadensis* which feeds on *Pl. maritima* and *Monochroa tetragonella*, feeding on *G. maritima*, reasons for their rarity are unknown. Also, the weevil *Mecinus collaris*, was rarely encountered during assessments of grazing management, possibly due to its life history, developing in flower stems of *Pl. maritima*, which makes it vulnerable to grazing. **For these species, it is imperative to gain additional information regarding their life history to optimize conservation efforts**.
4. **There are no species known as specialists on *Elytrigia atherica***. It was suggested that the halophilic picture-winged fly *Melieria picta* might feed monophagously on *E. atherica* (Smit 2010), but breeding attempts have failed (J.T. Smit pers com) and the species has also been found at places where no *E. atherica* was present (pers. obs.).
5. Other grasses (*Pu. maritima*, *F. rubra* and *A. stolonifera*) are generally common in grazed salt marshes, but the **short-grazed turf is suitable as habitat for only very few herbivores**. The herbivores feeding on these grasses have varying preferences for vegetation

height. While some species are exclusively found in taller swards, others prefer the fast growing grass under grazed conditions (Irmler and Heydemann 1985). Two endemic leafhopper species (*Aphrodes aestuarina* and *Anoscopus limicola*) and the rare endemic Psychid moth *Whittleia retiella* occur only in tall swards of *Pu. maritima* or *F. rubra* (Rickert 2011, chapter 4). Other species, such as the leafhoppers *Psammotettix putoni* and *Macrosteles sordidipennis* seem to prefer a shorter sward (Irmler and Heydemann 1985) and a warmer microclimate (chapter 4, box II)

6. Many **carnivorous species** (> 65 species) **and especially spiders show a clear preference for a specific vegetation structure** (chapter 3, chapter 4). On grazed marshes, many different species of money spiders (Linyphiidae) can be found, among which the habitat specialist species *Erigone longipalpis* and *Silometopus ambiguus*. Other species, such as the common halophilic wolf spider *Pardosa purbeckensis* and the endemic species *Praestigia* (formerly *Baryphima*) *duffeyi* reach highest densities in ungrazed marshes. The latter was found at highest densities in ungrazed, tall *Atriplex portulacoides* vegetation (chapter 3). A fifth species, the rare *Enoplognatha mordax*, was caught in very high densities in the moderately grazed tall vegetation of the grazed marshes at Noord-Friesland Buitendijks, but at other sites not enough individuals of this species were found to make a general statement about its habitat requirements.
7. **There is not much quantitative information on the effects of management on soil-microarthropods** (>18 species). In chapter 5 it was shown that compaction of previously uncompacted soil decreased soil fauna abundance by an order of magnitude, but on the long term, total abundance of soil microarthropods in the grazed marsh was not lower than in the control. Nevertheless, three halophilic species were more abundant in the *Elytrigia*-dominated ungrazed marsh than under moderate grazing.

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Plant nomenclature follows Van der Meijden (2005): *A(grostis) stolonifera; Arm(eria) maritima; Art(emisia) maritima; A(ster) tripolium; A(triplex) littoralis; A(triplex) prostrata; A(triplex) portulacoides; B(olboschoenus) maritimus; E(lytrigia) atherica; F(estuca) rubra; F(estuca) ovina; G(laux) maritima; J(uncus) gerardii; J(uncus) maritimus; L(imonium) vulgare; Pl(antago) maritima; P(lantago) coronopus; Pu(ccinellia) maritima*.

Sources of management data: I&H1985: Irmler & Heydemann 1985; I&H1986: Irmler & Heydemann (1986); M1995: Meyer et al (1995); M&R1996: Meyer & Reinke (1996); P2005: Pétillon et al. (2005); P2007: Pétillon et al. (2007); G2011: Georges et al. (2011); R2011: Rickert (2011); R2012: Rickert et al. (2012); F2013: Ford et al. (2013);, K&Sunpubl: Van Klink & Schrama unpublished data, Col Berg: Collection M.P. Berg.

Table B3.1 Preliminary list of 173 invertebrate species, among which 25 endemic (sub-)species, confined to coastal and inland salt marshes of north-western Europe. Given are the host-plant and habitat associations, red-list status, endemic status and response to grazing management, if known.
Red list status: su: susceptible; vu: vulnerable; en: endangered; cr: critically endangered; na: not available; id; insufficient data; conf: conflicing data; ext: extinct in Wadden Sea.
* species status disputed ** North sea basin + one more country ***North American species ****not confined to salt marshes in southern Europe

	Wadden Sea	Wadden Sea redlisted	North Sea endemic	host plant / habitat requirements		*Elytrigia* dominated	Ungrazed	Low	Moderate	High	source management response
Gastropoda											
PROSOBRANCHIA											
Assiminea grayana	y	*vu*	y**			?	+	+	-	-	M1995; K&Sunpubl
PULMONATA											
Ovatella myosotis	y	*vu*			id						K&Sunpubl
Amphipoda		na									
TALITRIDAE											
Orchestia gammarellus	y					+	+	?	-	-	I&H1986, F2013, metadata Ch3, Ch4, Ch5
Araneae											
DICTYNIDAE											
Argenna patula	y					+	+	?	+	-	P2005, Ch3, Ch4, metadata Ch5
LINYPHIIDAE											
Erigone arctica	y			high marsh/green beach	id						
Erigone longipalpis	y					-	-	?	+	+	P2007, F2013, Ch3, Ch4, Ch5
Praestigia duffeyi	y	*vu*	y	low marsh		?	+	?	-	-	Ch3, Ch4, M1995
Silometopus ambiguus	y					-	-	?	+	+	F2013, P2005, Ch3
THERIDIIDAE											
Enoplognatha mordax	y	*vu*				-	-	?	+	-	Ch3
LYCOSIDAE											
Arctosa fulvolineata	n					+	+	?	-	-	P2005, P2007
*Pardosa purbeckensis**	y				conf	+/-	+	?	+/-	-	Ch3, Ch4, Ch5 P2005,P2007, F2013

	Wadden Sea	Wadden Sea redlisted	North Sea endemic	host plant / habitat requirements	*Elytrigia* dominated	Ungrazed	Low	Moderate	High	source management response
Acari		na								
ORIBATIDA										
ORIBATELLIDAE										
*Oribatella littoralis**	y		?		=	=	?	=	?	metadata Ch5
AMERONOTHRIDAE										
Ameronothrus nigrofemoratus	y		?							
Ameronothrus schneideri	y		?							
HUMEROBATIDAE										
Zachvatkinibates quadrivertex	y		?							
MESOSTIGMATA										
ASCIDAE										
Antennoseius granulatus			?							
Antennoseius spinosus			?							
Cheiroseius salicorniae	y		?		-	+	?	+	?	metadata Ch5
Leioseius ibericus			?							
Leioseius salinus			?							
HALOLAELAPIDAE										
Halolaelaps nodosus	y		?							
Halolaelaps perfectus	y		?							
Halolaelaps coxalis	y		?							
RHODACARIDAE										
Rhodacarus salarius	y		?							
Rhodacarus inspectatus	y		?							
Rhodacarellus corniculatus	y		?							
DIGAMASELLIDAE										
Dendrolaelaps halophilus	y		?							
PARASITIDAE										
Vulgarogamasus trouessarti	y		?							

	Wadden Sea	redlisted	endemic	host plant / habitat requirements		*Elytrigia*	Ungrazed	Low	Moderate	High	source management response
Collembola		na									
Entomobryomorpha											
ISOTOMIDAE											
Archisotoma besselsi	y			pioneer zone		-	+	-	-	-	Col Berg
Archisotoma pulchella	y			pioneer zone		-	+	-	-	-	Col Berg
Archisotoma vareli	y	*y*	y	pioneer zone		-	+	-	-	-	Col Berg
Axelsonia littoralis	n			pioneer zone, oyster beds		-	+	-	-	-	Col Berg
Ballistura schoetti	y			low salt marsh		+	+	+	-	-	Col Berg
Folsomia sexoculata	y			low salt marsh		+	+	+	+	-	Col Berg
Halisotoma maritima	y			low salt marsh		+	+	+	-	-	metadata Ch5
Halisotoma poseidonis	y			low salt marsh		+	+	+	-	-	Col Berg
Isotoma riparia	y			low - middle salt marsh		-	-	+	+	+	metadata Ch5
Poduromorpha											
HYPOGASTRURIDAE											
Hypogastrura viatica	y			low salt marsh		+	+	+	-	-	Col Berg
NEANURIDAE											
Anurida tullbergi	y			low salt marsh, basalt rock dikes		-	+	-	-	-	Col Berg
Anurida maritima	y			pioneer zone, basalt rock dikes		-	+	-	-	-	Col Berg
Onychiuridae											
Thalassaphorura debilis	y			low - middle salt marsh		+	+	+?	-	-	metadata Ch5
Hemiptera		na									
Heteroptera											
MIRIDAE											
Conostethus griseus	y			*Limonium vulgare* & other halophytes			+	+	-	-	M1995; Ch4
Conostethus brevis	n			*Limonium vulgare*							
Conostethus major	n			*Limonium vulgare*							
Europiella decolor	y			*Artemisia maritima*			(+)		++	-	Ch4
Orthotylus moncreaffi	y			*Salicornia* spp.	id						Ch4
Orthotylus rubidus	y			*Salicornia* spp.	id						
Teratocoris saundersi	y			grasses, rushes, sedges							
LYGAEIDAE											
Henestaris halophilus	n			*Atriplex portulacoides*							
Henestaris laticeps laticeps	n			*Plantago coronopus*							

	Wadden Sea	redlisted	endemic	host plant / habitat requirements		*Elytrigia*	Ungrazed	Low	Moderate	High	source management response
Hemiptera (continued)											
SALDIDAE											
Salda littoralis	y				conf	-	+		+	-	Ch3; F2013
Saldula palustris	y				id						Ch3
Halosalda lateralis	y				id						Ch3
Chiloxanthus pilosus	y					-	-		+	+	Ch3
Saldula pilosella pilosella	y										
Auchenorrhyncha											
DELPHACIDAE											
*Prokelisia marginata*****	y			*Spartina* spp							
CICADELLIDAE											
Anoscopus limicola	y		y**	*Pu. maritima* (and other grasses?)		-	+		-	-	Ch4
Aphrodes aestuarina	y		y	*Pu. maritima* (and other grasses?)			+		-	-	Ch4
Eupteryx artemisiae	y			*Artemisia maritima*		-	-		+	-	host plant response
Macrosteles sordidipennis	y			*Pu. maritima*, *F. rubra*, *A. stolonifera*		-	-		+	-	I+H1985, metadata Ch5, box3
Paramesus obtussifrons	y			*Bolboscoenus maritimus*							
Psammotettix putoni	y			*Pu. maritima*, *F. rubra*, *A. stolonifera*		-	-		+	+	Ch4
Sternorrhyncha											
APHIDOIDEA											
APHIDIDAE											
Macrosiphoniella pulvera	y			*Artemisia maritima*		-					
Macrosiphoniella asteris	y			*Aster tripolium*		-	+	+	-	-	I&H1986
Staticomium limonii	y		y*	*Limonium vulgare*		-					
Aphis tripolii	y			*Aster tripolium*		-	+	+	-	-	I&H1986
Aphis longirostrata	y			*Pl. maritima*, *P. coronopus*		-					
Dysaphis maritima	y		y***	*Pl. maritima*, *P. coronopus*		-					
Coloradoa heinzei				*Artermisia maritima*		-					
Coloradoa submissa	y		y***	*Artermisia maritima*		-					
DREPANOSIPHIDAE											
Atheroides brevicornis	y			*Pu. maritima*, *F. rubra*		-	+	+	-	-	I&H1986
Sipha littoralis	y		y***	*Spartina* spp (+*Pu. maritima*, *F. rubra*)							
PEMPHIGIDAE											
Pemphigus trehernei	y		y	*Aster tripolium*							

	Wadden Sea	redlisted	endemic	host plant / habitat requirements	*Elytrigia*	Ungrazed	Low	Moderate	High	source management response
Lepidoptera		na								
TORTRICIDAE										
Eucosma lacteana	y			*Artemisia maritima*		-	-	+	-	R2011, Ch4
Eucosma tripoliana	y			*Aster tripolium*		+	+	-	-	R2011, Ch4
Eucosma rubescana	y			*Aster tripolium*		+	+	-	-	R2011
Phalonidia vectisana	y			*Triglochin maritima*					-	R2011
Phalonidia affinitana	y			*Aster tripolium*		+	+	-	-	R2011, Ch4
Bactra robustana	y			*Bolboschoenus maritimus*						
Lobesia littoralis	y			*Armeria maritima*	id	-				R2011
COLEOPHORIDAE										
Coleophora adjunctella	y			*Juncus gerardii*		-		+*	-	Ch4
Coleophora artemisiella	y			*Artemisia maritima*		-		+	-	ch4
Coleophora asteris	y			*Aster tripolium*		+		-	-	R2011
Coleophora atriplicis	y			*Atriplex* spp, *Salicornia* spp, *S. maritima*		+	+	+	+	R2011, Ch4
Coleophora glaucicolella	y			*Juncus gerardii*						
Coleophora maritimella	y			*Juncus maritimus*						
Coleophora salinella	y			*Atriplex* spp						
Coleophora salicorniae	y			*Salicornia* spp						
Coleophora adspersella	y			*Atriplex* spp, *S maritima*						
Coleophora deviella	y			*Suaeda maritima*		+	+	-	-	R2011
Goniodoma limoniella	y			*Limonium vulgare*	id					R2011
GELICHIIDAE										
Aristotelia brizella	y			*Armeria maritima* (+*Limonium vulgare*)	id					R2011
Monochroa moyses	n			*Bolboschoenus maritimus*						
Monochroa tetragonella	y			*Glaux maritima*	id					R2011
Scrobipalpa instabilella	y			*Atriplex portulacoides*		+	+	+	-	R2011
Scrobipalpa nitentella	y			*Atriplex* spp		+		-	-	R2011, Ch4
Scrobipalpa salinella	y			*Salicornia* spp, *S. maritima*, *A. tripolium*		+	+	+	-	R2011, Ch4
BUCCULATRICIDAE										
Buccultrix maritima	y			*Aster tripolium*		+	+	+	-	I&H1986, R2011, Box1
PTEROPHORIDAE										
Agdistis benetii	y			*Limonium vulgare*		+	+	-	-	R2011

	Wadden Sea	redlisted	endemic	host plant / habitat requirements		*Elytrigia*	Ungrazed	Low	Moderate	High	source management response
Lepidoptera (continued)											
PYRALIDAE											
Agriphila selasella	y			*Pu. maritima*, *F. ovina*							R2011
Pediasia aridella	y			*Puccinellia maritima*			-	+	+	+	R2011
ELACHISTIDAE											
Elachista scirpi	y			*Bolboschoenus maritimus*							
PSYCHIDAE											
Whittleia retiella	y		y	*Pu. maritima*, *F. rubra*			+	+	+	-	R2011, Ch4
NOCTUIDAE											
*Mythimna favicolor**	y		y	*Puccinellia maritima*							
Cucullia asteris	y			*Aster tripolium*							
Coleoptera											
CARABIDAE											
Acupalpus elegans	y	*cr*			id						Ch3
*Bembidion minimum****	y					-	-		+	+	I&H1985, P2007,F2013,Ch3, Ch4
Bembidion normannum	y	*vu*				+/-	+/-	+/-	+/-	+/-	G2011, Ch4
Bembidion ephippium	n?	*cr*									
Bembidion tenellum	ext										
Bembidion iricolor	y	*vu*			conf		+/-		-	-	P2007, F2013
Cillenus lateralis	y	*en*		mud / sand flats							
Dicheirotrichus gustavii	y				conf	+/-	+/-	+/-	+/-	+/-	I&H1985, G2011, F2013, Ch3, Ch4
Dicheirotrichus obsoletus	n					+/-	+/-	?	?	?	G2011
Dyschirius salinus	y			Sandy soil	id						M&R1996
Dyschirius salinus ssp. *Salinus*	y		y								
Dyschirius chalceus	y	*en*		Sandy soil							
Pogonus chalceus	y	*su*			conf	+/-	+/-	+/-	+/-	+/-	G2011, Ch3, K&S unpubl
Pogonus luridipennis	y	*vu*		mud flats	id	-					G2011, Ch3
Pogonus littoralis	n			mud flats	id	-					G2011, P2008
Tachys scutellaris	n										
STAPHYLINIDAE											
Meotica winkleri	y	*cr*									
Atheta vestita	y				id						Ch4

	Wadden Sea	redlisted	endemic	host plant / habitat requirements		*Elytrigia*	Ungrazed	Low	Moderate	High	source management response
Coleoptera (continued)											
STAPHYLINIDAE											
Bledius bicornis	y			Sandy soil							
Bledius diota	y	*en*	y	Sandy soil							
Bledius furcatus	y	*en*		Sandy soil							
Bledius limicola	y			Sandy soil							
Bledius spectabilis	y	*vu*		Sandy soil							
Bledius subniger	y			Sandy soil							
Bledius tricornis	y	*vu*		Sandy soil		?	-	-	+	+	M1995
Bledius unicornis	n										
Brachygluta helferi	y					+	+		-	-	metadata Ch5
Brachygluta simplicior	n										
Brachygluta waterhousei	n										
Brundinia marina	y					=	=	=	=	=	F2013, Ch4, metadata Ch5
Brundinia meridionalis	y	*su*									
Carpelimus foveolatus	y										
Carpelimus halophilus	y	*en*			id						Ch4
Carpelimus schneideri	y	*en*									
Diglotta mersa	y	*en*									
Diglotta sinuaticollis	y										
Halobrecta algae	y										
Halobrecta algophila	n										
Halobrecta flavipes	y	*su*			id						Ch4
Heterothops binotatus	y	*vu*									
Ochthephilum collare	y										
Philonthus binotatus	y										
Philonthus dimidiatipennis	n										
Philonthus salinus	y	*su*									
Quedius simplicifrons	y	*su*				+/-	+/-		+/-		metadata Ch5
Stenus intermedius	y										
Tomoglossa brakmani	y		y								
Tomoglossa heydemanni	y	*cr*	y								

	Wadden Sea	redlisted	endemic	host plant / habitat requirements		*Elytrigia*	Ungrazed	Low	Moderate	High	source management response
Coleoptera (continued)											
HETEROCERIDAE											
Heterocerus fossor	n										
Heterocerus flexuosus	y	*vu*			id						
Heterocerus obsoletus	y	*en*									
Heterocerus maritimus	y	*vu*			id						
Heterocerus aureolus	n		y								
CURCULIONIDAE											
Mecinus collaris	y	*su*		*Plantago maritima*	id						Ch4
Pelenomus zumpti	y	*vu*		*Glaux maritima*		-	-		+	+	Ch4
Trichosirocalus thalhammeri	y	*en*		*Plantago maritima*		-	-		+	+	Ch4
Polydrusus pulchellus	y	*en*		*Atriplex portulacoides*	id						Ch4
BRENTIDAE											
Pseudaplemonus limonii	y	*en*		*Limonium vulgare*							
HYDRAENIDAE											
Ochthebius auriculatus	y	*vu*	y			-	-	+	+	+	I&H1986, Ch4
Ochthebius marinus	y										
Ochthebius viridis	y	*vu*									
LIMNICHIDAE											
Bothriophorus atomus	ext	*ext*									
CANTHARIDAE											
Cantharis rufa ssp. darwinia	y		y			+	+		-	-	F2013, Ch4, metadata Ch5
COCCINELLIDAE											
*Nephus limonii**	y	*su*	y		id						
LATRIDIIDAE											
Corticaria crenulata	y										
MORDELLIDAE											
Mordellistena nanuloides	n		y	*Artemisia maritima*							
ANTHICIDAE											
Cyclodinus constrictus	y										
Cordicollis instabilis	y										

	Wadden Sea	redlisted	endemic	host plant / habitat requirements	*Elytrigia*	Ungrazed	Low	Moderate	High	source management response
Coleoptera (continued)										
CHRYSOMELIDAE										
Phaedon concinnus	y	*su*	y	*Cochlearia* spp, *Triglochin maritima*						
Longitarsus plantagomaritimus	y	*vu*	y	*Plantago maritima*	-	+	-	-	-	M&R1996
Hymenoptera										
APIDAE										
Colletes halophilus	y		y	*Aster tripolium* + sandy soil						
Epeoplus tarsalis ssp. *Rosenburgensis*	n	*nl*	y							
Diptera										
TEPHRITIDAE										
Campiglossa plantaginis	y			*Aster tripolium*	?	+	+	+/-	-	R2011, Box I, Box II
ULIDIIDAE										
Herina palustris	y									
Melieria cana	y									
Melieria picta	y			unclear						
STRATIOMYIDAE										
Nemotelus uliginosus	y									
Nemotelus notatus	y				?	-	-	+	+	M1995
AGROMYZIDAE										
Micromorphus albipes	y				?	-	-	+	-	M1995
Melanagromyza tripolii	y			*Aster tripolium*		+	+	-	-	host plant response
Phytomyza asteris	y			*Aster tripolium*		+	+	-	-	host plant response
CHLOROPIDAE										
Tropidiscinis junci	y	?		*Juncus gerardii*						
meromyza puccinelliae	y			*Puccinellia maritima*						
LIMONIIDAE										
Symplecta stictica	y				?	-	-	+	+	I&H1986; M1995
CECIDOMYIIDAE										
Jaapiella Schmidti	y									
Mayetola puccinelliae	y				?	-	+	+	-	M1995

Chapter 8

General synthesis

Roel van Klink

Grazing by large herbivores can maintain plant species richness and prevent succession to botanically species-poor, tall vegetation. Among the grassland types of Western Europe, salt marshes are unique, as their natural succession does not lead to forest, but to tall herbaceous vegetation, dominated by the mat-forming grass *Elytrigia atherica* or the dwarf-shrub *Atriplex portulacoides* (Olff et al. 1997, Schrama 2012). This natural succession, however, leads to a decrease in plant species richness, at least at small scales (Bakker 1978, Bakker et al. 2003, Wanner et al. 2014).Therefore some form of management, usually in the form of livestock grazing, is often considered necessary.

Although the effects of grazing management on plant communities have been researched extensively, and the mechanisms behind its success are well understood, its effects on communities of arthropods and also birds have received much less attention, However, due to the different spatial and temporal scales animals operate on, it is likely that other mechanisms apply for animal than for plant communities. The aim of this thesis was, therefore, to assess the effects of grazing by large herbivores on salt-marsh arthropod communities and to translate this knowledge into practical management recommendations and some options for time and cost effective monitoring of arthropod communities. To understand how arthropod communities on salt marshes are affected by large herbivores, I followed a mechanistic approach. In chapter 2 a framework of the mechanistic pathways by which large herbivores affect arthropods was proposed, and the evidence for each pathway was presented. All chapters of this thesis are represented by this framework (Fig. 8.1), and especially in chapters 4 and 5 an attempt was made to fill some of the knowledge gaps identified in chapter 2.

THE IMPORTANCE OF STRUCTURAL VEGETATION COMPLEXITY

In chapter 2 we used meta-analytical techniques to show that arthropod species richness generally responded more negatively and often opposite to grazing than plant species richness. This was confirmed in chapter 4, where plant species richness increased under grazing, while arthropods were most abundant and species rich in tall, ungrazed vegetation. This difference in the response of plant and arthropod species richness can, to a large extent, be explained by the importance of the structural complexity of vegetation and resource quantity (biomass) for arthropod species richness (Morris 2000, Bell et al. 2001, chapter 2). The importance of vegetation structure was reflected throughout this thesis, playing a role in every single chapter.

Vegetation structure describes the architectural complexity of the vegetation, which, for arthropods determines to a large extent how many species can occur per unit area or per individual plant (Morris 1967, 2000, Tallamy and Denno 1979, Lawton 1983). Moreover, the number of specialised herbivorous insect species per plant species is strongly determined by the size and architectural complexity of the plant (Lawton and Schroder 1977, Tscharntke 1997). Through defoliation and to a lesser extent by trampling and defecation, large herbivores can change the architectural complexity of vegetation in multiple

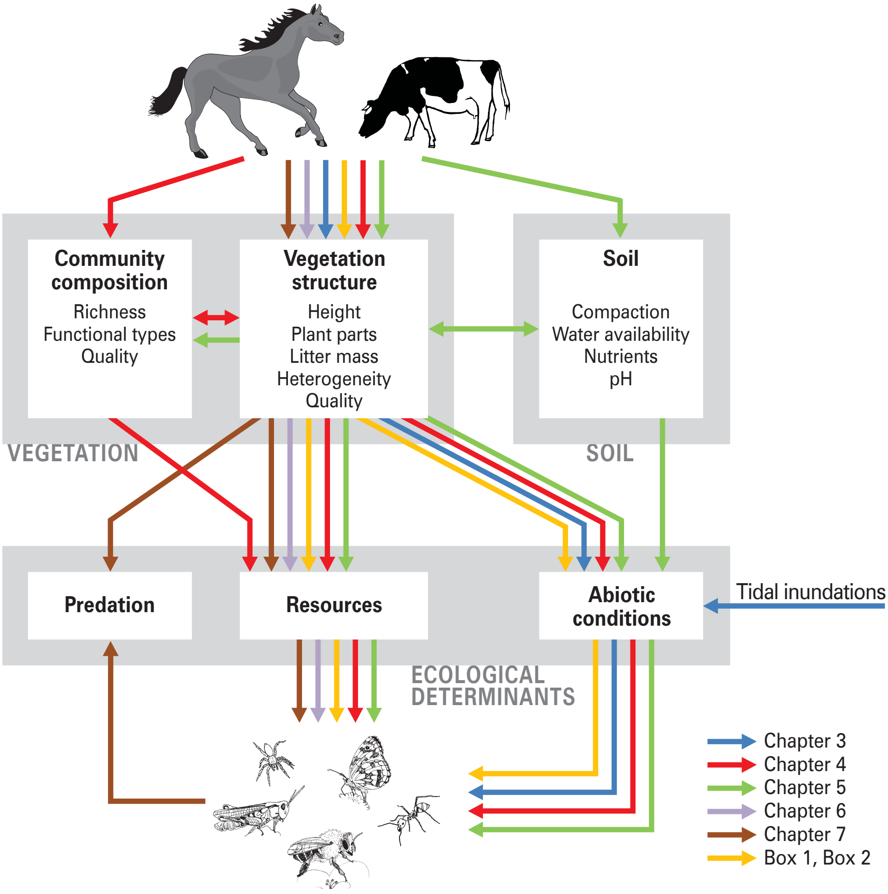

Figure 8.1 Investigated pathways for all chapters and boxes in the framework of chapter 2.

ways. First and most obviously, defoliation by large herbivores decreases canopy height, which strongly decreases structural complexity of the vegetation, and often leads to the loss of certain plant organs, such as flowers (Morris 2000). Secondly, by grazing selectively, large herbivores may create a patchwork of short, grazed vegetation and tall ungrazed vegetation (Bakker et al. 1984, McNaughton 1984, Berg et al. 1997, Adler et al. 2001, chapter 4).

On salt marshes, there is a strong difference between the arthropod communities of short grazed vegetation and tall, ungrazed vegetation (chapter 3, 4, 5), which causes contrasting patterns of α- and β-species richness along the inundation gradient (chapter 3). While in short grazed vegetation, only few species persist, tall ungrazed vegetation generally harbours more species, among which many habitat generalists (Andresen et al. 1990, Pétillon et al. 2005, chapter 3,4). Presumably, these inland species can persist here because in this tall vegetation the physical stress of inundations is ameliorated (Pétillon et al. 2005), and lower soil salinity (Bakker 1985, Esselink et al. 2002, chapter 5). Also, a large number of salt-marsh specialist species reached highest densities in tall, ungrazed vegetation, even under the dominance of the tall grasses *E. atherica* and the mat-forming *Festuca rubra* (chapter 4). Especially soft-bodied arthropod groups such as spiders (Pétillon et al. 2007, chapter 4), moths (Rickert et al. 2012, chapter 4) and leafhoppers (Irmler and Heydemann 1985, chapter 4) reached higher species richness in ungrazed marshes. These groups therefore seem to be especially detrimentally affected by grazing, while many beetle species seem to be more tolerant, or even positively affected (Pétillon et al. 2007, chapter 4).

Changes in vegetation structure caused by grazing have strong consequences for plants and their herbivorous insects. When vegetation, and in particular grasses, increase in height, the amount of bare soil decreases, and shading increases in the lower vegetation strata. This causes a decrease in plant species richness, as colonisation possibilities for annuals become limited and short-statured perennials will suffer from light competition (Olff and Ritchie 1998). Consequentially, herbivorous insects associated with these plants will also disappear, as was shown in chapter 4. Conversely, we showed that experimental defoliation can open the canopy and allow colonisation by short-statured plants, thus leading to vegetation resembling a grazed salt marsh (chapter 5). This was especially evident when combined with soil compaction, which created patches of bare soil and increased soil salinity.

The structure of individual plants can also be changed dramatically by large herbivores. This is especially important for herbivorous insects living on plants that are palatable for livestock, such as *Aster tripolium*. Host plant biomass was found to be the most important driver for the abundance and species richness of herbivorous insects living on *A. tripolium* (box I, box II). Moreover, flower-visiting insects were most abundant under grazing treatments where flower abundance of A. tripolium and other tall Asteraceae was highest (chapter 6), while the number of flowers of the short-statured species *Glaux maritima* and *Potentilla anserina* was irrelevant for insect abundance.

With respect to the tall, but to livestock unpalatable, forb *Artemisia maritima*, it was shown that biomass was of high importance for the herbivorous insects associated especially with mature plants (chapter 4). In the manipulative experiment of box II, however, it became clear that during establishment, *A. maritima* and its associated herbivorous insects were clearly negatively affected by shading from the surrounding vegetation. Plant architecture of the short-statured grasses *Puccinellia maritima* and *Festuca rubra* was of less importance for their associated herbivorous fauna than microclimate, which was determined by the surrounding vegetation.

Also for insectivorous grassland birds, horizontal heterogeneity in vegetation structure was hypothesised to be an important factor determining habitat suitability, as vegetation height is tightly linked to the availability and accessibility of invertebrate prey (Vickery et al. 2001). Experimental evidence for this is, however, limited, and a positive relation of bird abundance with structural vegetation heterogeneity was only found by Milsom et al. (2000), while other researchers reported a negative relation of bird abundance with mean vegetation height (Atkinson et al. 2004, 2005). In the grazing experiment at Noord Friesland Buitendijks, vegetation heterogeneity was indeed confirmed as important for nest-site choice of Redshank (*Tringa totanus*) and Oystercatcher (*Haematopus Ostralegus*) (Mandema et al. in press), but, surprisingly, Meadow pipits (*Anthus pratensis*) were found to forage preferentially in relatively homogeneous vegetation (chapter 7). The importance of grazing induced patchiness for arthropods and their predators clearly requires more study, since it is currently poorly known if, when, and how, this form of heterogeneity can have positive effects on diversity and species abundances.

CONSERVATION MANAGEMENT

The aim of conservation management is to ensure that the target species of a community can maintain population densities large enough to survive (Shaffer 1981). Especially when populations fluctuate severely, maintaining sufficiently large populations is important because small populations are more vulnerable to environmental stochasticity, (Shaffer 1981, Lande 1988, Pimm et al. 1988). Additionally, small populations will suffer from inbreeding depression, leading to a decline in population fitness and a decrease in genetic variation within the population (Shaffer 1981, Saccheri et al. 1998).

This raises the question, how large populations have to be to survive. The minimum viable population size was estimated at around 5000 individuals, mostly based on vertebrates (Traill et al. 2007, 2010). Few estimates have been made for terrestrial invertebrates, but these range around 10,000 individuals (Traill et al. 2007). The minimum viable population size might differ severely between invertebrate species, as they vary strongly in reproductive output and mobility. It is therefore also important to consider the spatial extent of a population, and if individuals can find each other to reproduce. For the usually small-sised invertebrates, the spatial extent at which a sufficient number of individuals must be present is logically much smaller than for large, mobile species.

But even when a population of a species is below its minimum viable population size, it does not necessarily go extinct directly. Many populations can continue to exist until some stochastic event or a decline in fitness pushes them over the edge, a phenomenon called extinction debt (Tilman et al. 1994, Hylander and Ehrlén 2013). This extinction debt poses serious difficulties in predicting the consequences of conservation management for populations, and therefore demands good knowledge of the relations between management, habitat quality and population dynamics.

Effects of grazing management for the conservation of salt-marsh arthropods, plants and birds

The aim of salt-marsh conservation management should be to ensure that populations of all species native to this habitat, and especially those restricted to it, can sustain viable population sizes. Given the detrimental effects of abandonment for many arthropod and bird species, and the equally detrimental effects of grazing for other species (box III, Mandema 2014) it is clear that in all likelihood it will be impossible to accommodate all species using a single management regime (see also chapter 4). Therefore, both grazed and ungrazed salt marshes are of conservation interest, which raises the question ***how*** grazing should be applied. Here, I will sum up the evidence for the consequences of different grazing options for the conservation of arthropods, while considering plants and birds as well.

CESSATION OF GRAZING

It is well known and understood that the cessation of grazing as well as the natural succession of salt marshes will, ultimately, lead to the dominance of a few tall plant species and a decrease in plant species richness, at least at small spatial scales (Bakker 1989, Bakker et al. 2003, Veeneklaas 2013, Wanner et al. 2014). This dominance is, however, rarely total, and often pockets of species-rich vegetation remain, especially in places with poor drainage (Veeneklaas 2013).

Still, even after long-term cessation of grazing, ungrazed salt marshes contained high species richness of both salt-marsh specialist and generalist arthropods (Pétillon et al. 2007, Rickert et al. 2012, chapter 3, 4) and birds (Mandema 2014), but this is usually accompanied by a large difference in species composition between grazed and ungrazed salt marshes (chapter 3, 4, Mandema 2014). After cessation of grazing many short-statured plant species and their associated fauna, as well as many carnivorous arthropod species and birds disappear, and are replaced by species with a preference for tall vegetation. It is currently unclear whether this process can be reversed after dominance of botanically poor tall vegetation has established. Therefore, livestock grazing seems to be one of the few alternatives to maintain high species richness of plants, arthropods as well as birds.

CHOICE OF LIVESTOCK SPECIES

In the grazing experiment at Noord-Friesland Buitendijks strong behavioural differences were found between horses and cattle. Horses were found to be more active, have higher intake rates and eat more fibre rich vegetation than cattle (Nolte 2014). It was surmised that in terms of weight and intake rate, one horse equals 1.7 cattle (Nolte 2014), making the comparison between treatments problematic. Due to their higher activity, trampling risk for bird nests is also higher under horse grazing than under cattle grazing (Mandema et al. 2013). Despite these differences, we found few indications that the choice of livestock species has consequences for arthropods (chapter 6), especially when differences in weight and intake rate are considered. This agrees with literature, where only a very limited number of studies have shown evidence of differences in the effects of different livestock species on arthropod communities (Carvell 2002, Öckinger et al. 2006), while the majority of studies found no difference between herbivore species (Prendini et al. 1996, Samways and Kreuzinger 2001, Rosa-García et al. 2009a, b) or breeds within species (WallisDeVries et al. 2007, Jáuregui et al. 2008). Moreover, it is unclear whether the reported differences between species may have been confounded with stocking density or intake rate.

Still, for highly palatable plant species such as *A. tripolium* and their associated herbivorous fauna, differences in selectivity between livestock species may have consequences. Among the most commonly used livestock species, sheep are most selective, and consume

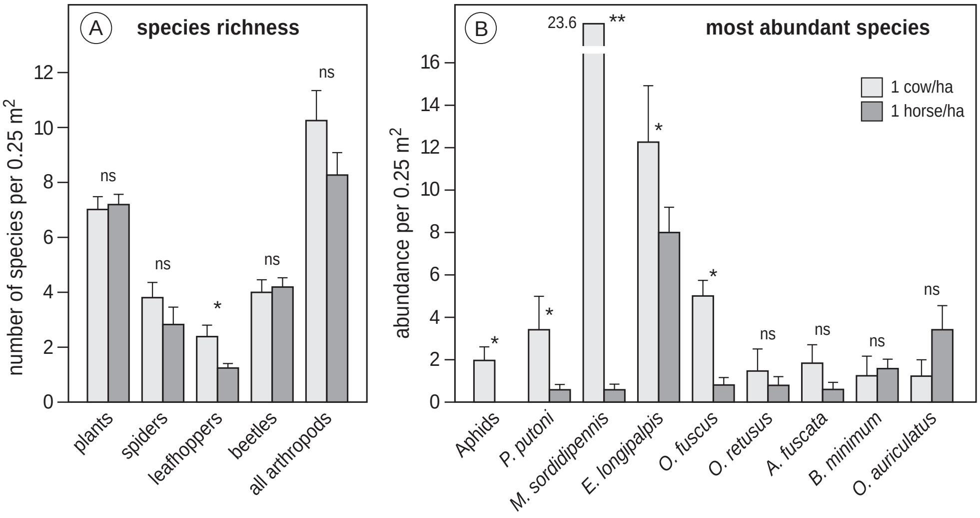

Figure 8.2 Comparison of plant and arthropod species richness and abundance of the most common arthropod species per 0.25 m^2 in the typical short-grazed sward under horse grazing (4 cm) and cattle grazing (8 cm) at a density of 1 animal ha^{-1}. Samples were taken by suction sampling with biomass removal (following the method described in chapter 2) in five replicate 0.25 m^2 perspex enclosures, after which two pitfalls were placed in each enclosure (see chapter 5) and the enclosure was covered with gauze. The pitfalls were emptied after eight days. Species: Leafhoppers: *Psammotettix putoni*, *Macrosteles sordidipennis*; Spiders: *Erigone longipalpis, Oedothorax fuscus, Oedothorax retusus*; beetles: *Atomaria fuscata*, *Bembidion minimum*, *Ochthebius auriculatus*. $^*p < 0.05$; $^{**}p < 0.01$; ns: not significant.

high amounts of A. tripolium (Kiehl et al. 1996), which at intermediate to high stocking densities is highly detrimental to moths developing on this plant (Rickert 2011). Cattle were found to consume large amounts of *A. tripolium* as well, while horses consumed more fibre-rich plants (Nolte 2014), but caused severe damage by trampling (Nolte et al. 2013). Herbivores of A. tripolium reached highest abundances (Rickert 2011) and species richness per plant (box I) in ungrazed marshes.

A simple comparison of arthropod abundance in the typically short-grazed sward under high density horse grazing with the typically rougher sward under cattle grazing at the same density (1 animal ha^{-1}), shows that total arthropod abundance under horse grazing was one third of that under cattle grazing (cattle: 57.6 ind. per 0.25 m^2; horse: 19.2 ind. per 0.25 m^2, GLM: $t = -6.4$, $p < 0.001$), but no significant difference in total species richness (Fig. 8.2A). Moreover, most species were more abundant under cattle grazing, though mostly not significantly (Fig. 8.2B). This clearly shows that at the same stocking density, horse grazing is more detrimental to arthropods than cattle grazing, but it is unclear whether these differences would be found when corrected for weight and intake rate per hectare.

To conclude, it is evident that intensive horse grazing is highly detrimental to arthropod species richness and abundance, but it is likely that this is to a large extent caused by the higher weight, intake rate and trampling activity of horses in comparison to cattle, leading to a greater impact on soil and vegetation at a similar stocking density. Nevertheless, when corrected for weight and intake rate, horse grazing is in all probability somewhat more detrimental to invertebrate communities than either sheep or cattle grazing, due to the intense trampling.

CHOICE OF STOCKING DENSITY

As there is strong evidence that differences in stocking density have a strong impact on arthropod communities on salt marshes and other ecosystems (chapter 2, 4, 6), and that differences found between livestock species are in most cases minimal in comparison to differences in stocking density (see previous section), the most important decision to make regarding the application of grazing management is at which stocking density to graze. Here, I will summarise the consequences of different stocking densities for communities of salt-marsh arthropods, plants and birds.

Grazing with high stocking densities (1 horse / 1.5 cow /10 sheep ha^{-1}) has no conservation benefit for arthropods. There is an overwhelming amount of evidence showing that grazing at high stocking densities is highly detrimental to species richness of arthropods in all ecosystems, and only few studies have shown otherwise. This was already stated by Morris (Morris 1967) for chalk grasslands and is still true in 2013 for salt marshes. However, in the experiment on the salt marshes of Noord-Friesland Buitendijks, in the winter of 2012 the highest number of both solitary and flocking birds was observed under highest stocking densities (Mandema 2014), suggesting that this grazing regime has some attraction to birds. Nevertheless, densely stocked paddocks had a homogeneous vegetation structure (Nolte 2014) and no Meadow Pipit nests were found under this management (chapter 7) . Mandema (2014) suggested that site-fidelity of long-lived birds may cause the persistence of breeding under less than favourable conditions, making highly stocked sites effectively an ecological trap. Only geese were consistently more abundant under intensive grazing regimes, especially in autumn (Bos et al. 2005, Mandema 2014), which benefit from the nutrient-rich regrowth of vegetation (Ydenberg and Prins 1981, Bos et al. 2005).

Grazing at moderate stocking densities (≈0.5 horse/ 4 sheep/ 1 cow ha^{-1}) on salt marshes will create a patchwork of short and tall vegetation (Berg et al. 1997, Versteegde 2011, chapter 4), and an early developmental stage of patchiness can be witnessed in the grazing experiment at Noord Friesland Buitendijks (Nolte 2014). A heterogeneous sward has often been suggested to be highly beneficial to birds (Vickery et al. 2001) and arthropods (Dennis et al. 1998, Joern 2005), but experimental evidence is scarce. Although in chapter 4 it was shown that grazed vegetation mosaics undoubtedly harbour more arthropod species than homogeneous short-grazed swards, not all species present at a site could be accommodated under grazing with moderate stocking densities. Furthermore, no evidence was found that a patchy vegetation structure is necessarily beneficial for the foraging success of Meadow Pipits (chapter 7), although Redshank and Oystercatcher chose their nest locations preferably in patchy vegetation (Mandema et al. in press).

There is not much knowledge about the effects of long-term grazing at low stocking densities (≈ 1-3 sheep/ 0.5 cow ha^{-1}) on salt marshes. Rickert (2012) showed that after 20 years of grazing at low stocking densities on German marshes, moth species richness was higher than under moderate or high densities, and was at least as high as in ungrazed salt marshes. Nevertheless, under this grazing regime, large parts of the marsh were dominated by *E. atherica*, especially the higher elevated parts (Esselink et al. 2009), and this is likely to also occur on other salt marshes. Grazing at low stocking densities seems a promising option for arthopod conservation if partial dominance of *E. atherica* is considered acceptable.

ROTATIONAL GRAZING[1]

Rotational grazing with fallow periods of one year (or more) has been coined as a management option that can optimise conservation benefit for arthropods and other organisms by creating or restoring temporal heterogeneity in conditions (see also chapter 2). During fallow years, populations of vulnerable plant and arthropod species can reach high reproductive output, buffering them against the more adverse conditions during grazed years. During these grazed years, other species may benefit, and the spread of competitive grasses can be stemmed. So far, all lines of evidence, and several studies performed in calcareous grasslands and upland pastures (Morris et al. 2005, Farruggia et al. 2012, Scohier et al. 2013) suggest that rotational grazing will indeed have highly beneficial effects on arthropod communities (chapter 6), although dominant tall grasses may gradually increase in cover (Nolte 2014).

For the application of rotational grazing management, several issues need to be considered. Firstly, the stocking density used during grazed years will to a large extent determine the survival probability of the arthropod populations built up during ungrazed years. If all vegetation is grazed to the ground during grazed years, most populations will not survive and for most species rotational grazing will have no beneficial effects. Secondly, cover of *Elytrigia atherica* will most likely increase under this type of management, as was tentatively shown in the experiment at Noord-Friesland Buitendijks (Nolte 2014). Although such an increase in tall vegetation will undoubtedly increase arthropod abundance and species richness, it is worth questioning to what extent this development would be desirable, especially since its future consequences are unknown. Lastly, it should be considered how long the ungrazed period will last. In a study in German upland grasslands it was shown that stem-borers of *Dactylis glomerata* needed at least two ungrazed years to increase population sizes (Rothenwöhrer et al. 2013), showing that yearly rotations are not necessarily sufficient to benefit all arthropod species. On the other hand it is likely that competitive grasses, and most notably *E. atherica*, will increase strongly during ungrazed periods, possibly displacing short-statured species. Monitoring will be necessary to determine when this is imminent and grazing should then be reinstated, since so far,

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[1] Rotational grazing for conservation benefit should not be confused with rotational grazing maximising agricultural output. In the latter system, grazing pressure is extremely high for a short period, after which livestock is relocated to the next field (e.g. Undersander et al. 2002). There is no evidence to suggest that this type of grazing has any nature conservation interest.

only a non-significant decrease in plant species richness was found after four years of rotational grazing (Nolte 2014). More research and practical experience are necessary to validate the conservation potential of this type of management.

Conflicting requirements

The highly conflicting responses of invertebrate (box III), plant (Nolte 2014), and bird species (Mandema 2014) (summarised in Table 8.1) to grazing management suggest that it will be impossible to sustain all species under a single type of management. I therefore recommend several grazing regimes including abandonment to be present at all times. As stated above, grazing at high stocking densities has no conservation value for arthropods, but all other regimes have value for some species. Hence, a mosaic should be installed of permanently ungrazed areas and areas with grazing at moderate densities, low densities and rotational grazing.

Grazing at high densities may incidentally be necessary to return tall vegetation to a shorter state and to decrease the spread of *E. atherica*, but it should be remembered that most species of invertebrates will be lost by this type of management, probably even if it is only applied for one year. If recolonization of species from nearby source habitats after high density grazing is possible, pressure grazing might be a suitable option to decrease the dominance of single plant species.

Table 8.1 Summarised effects of different stocking densities (live stock units) on varying groups of organisms. This table is based on De Vlas et al. (2013), with new insights added

stocking density (LSU)	ungrazed 0	high >1	moderate 0,5	low 0,2	rotational (0/1)	source
plant species richness	--	+	+	-	-	Nolte et al in prep
reduction *E. atherica*	--	+	0	-	-	Nolte 2014
vegetation height	++	--	0	+	++	Nolte 2014
patchiness	--	--	+	+	?	Nolte 2014 / ch 4
flower-visiting insects	++*	--	0	+	++/0	ch 6
insects on *A. tripolium*	-*	--?	-	?	++/?	box I
arthropod abundance	++	--	0	++	+	ch 4, ch 5, fig 8.2, Rickert et al. 2012
arthropod species richness	++	--	0	++	+	ch 4, ch 5, fig 8.2, Rickert et al. 2012
suitability for geese	--	++	0	-	-/+	Mandema 2014
bird species richness	?	+	0	0	0	Mandema 2014
trampling of nests	--	++	+	-	-/+	Mandema 2014

*based on one replicate on one marsh

Monitoring of arthropod communities

When conservation management is applied, it is important to monitor the effectiveness of this management for the target species and/or communities. Monitoring of populations of arthropods and other invertebrates is time and labour intensive and requires a large amount of taxonomic knowledge (box III). For this reason it is practical to monitor habitat suitability for arthropods using easily measurable proxy variables or bioindicators. The use of these proxy-variables should be based on sound scientific evidence (a good example is given by Maes and Van Dyck 2005).

Unfortunately, as was shown in chapters 2 and 4, response of plant species richness to grazing management is a poor and often contradictory predictor for response of arthropod species richness. Moreover, every species has a unique response and tolerance to changes in its environment, and hence, responses are rarely transferable between species (box III). Also, species richness of different animal taxa rarely shows good correlations (Vessby et al. 2002, Fleishman and Murphy 2009, Fattorini et al. 2011, Mandelik et al. 2012, but see Duelli and Obrist 1998, see Rossi 2011 for a critique) suggesting limited usefulness of diversity assessments for one taxon only.

During this study some proxy-variables emerged which appear to be reliable indicators of habitat suitability for a number of arthropod species. Unfortunately, these indicators apply to only few of the large number of invertebrate species indigenous to salt marshes, and it is unlikely that they are representative for other species. Further work will be necessary to find and test additional comprehensive indicators.

For the occurrence of specialised herbivorous insects, obviously, the presence of their host plant is the first prerequisite for their occurrence. The presence of a host plant, however, does not guarantee the presence of its herbivores (Rickert et al. in prep). This can, in some cases, be attributed to dispersal limitation, but in grasslands it is often the case that the host plant is simply not suitable for the herbivore, either because certain structures are missing (Morris 2000), because microclimate is unfavourable (e.g. Thomas et al. 1986), or because of high levels of direct ingestion of arthropods (Van Noordwijk et al. 2012). In chapter 4, good correlations between host plant cover and insect abundance were found for *Artemisia maritima* and *Juncus gerardii* (Table 4.2), suggesting that this is a good indicator for habitat suitability of its herbivores. Some caution is in order though, since *J. gerardii* is consumed by cattle (and possibly horses) (Bakker et al. 2008), whereas it seems to be avoided by sheep and geese (per sobs). For most other plant species, in particular grasses, cover percentage was a poor, and sometimes even negative predictor for insect abundance (Table 4.2), showing poor indicator potential.

Aster tripolium is palatable to both livestock and herbivorous insects (Nolte 2014, box I, box II). Because biomass and flower abundance are reduced by livestock (Nolte et al. 2013), this decreases the resource base for both herbivorous and flower visiting insects.

Monitoring the flower abundance of *A. tripolium* can potentially be a time and cost effective way of monitoring habitat quality for a significant number of arthropod species. Floral abundance should be measured in two ways:1) an estimate of *A. tripolium* flower abundance over the area (in chapter 6 measured as 20 4 m^2 quadrats in a linear transect across each paddock, estimated in abundance classes), and 2) the number of flower heads per plant (, 2). In chapter 6, abundance of all flowering Asteraceae per transect was shown to correlate very well with total pollinator abundance ($R^2 = 0.9$), and flower abundance of *A. tripolium* alone correlated somewhat less well ($R^2 = 0.74$). On botanically richer salt-marshes, the importance of other flowering plant species such as *Limonium vulgare* and *Armeria maritima* for flower-visiting insects should first be investigated. In box I it was shown that total flower abundance was a good predictor of plant weight, insect abundance and insect species richness (Fig. B1.4), although variation was large. In general, small individuals of *A. tripolium* harboured few individuals and species of herbivorous insects, but not all tall individuals accommodated many individuals or species. To maximise conservation success, the presence of tall, undamaged plants is therefore important. A decrease in flower abundance can be expected to decrease numbers of flower visiting insects and herbivorous insects on *A. tripolium*, but this should not be expected to have predictive value for other, especially shorter plant species (see also box II).

CONCRETE MANAGEMENT RECOMMENDATIONS FOR THE CONSERVATION OF SALT-MARSH ARTHROPODS

In summary, I make the following recommendations for the conservation management of salt marshes for arthropod species richness. These may, however, conflict with the requirements of birds or plants (Table 8.1). Details of the response of different arthropod species and groups are given in box III.

- **Grazing with high stocking densities** (1 horse / 1.5 cow / 10 sheep ha^{-1}) **has no conservation value for arthropods**.
- **Unmanaged salt marshes, even those dominated by *Elytrigia atherica* or *Atriplex portulacoides* have conservation value** for a number of species, among which the North-Sea endemic spider *Praestigia duffeyi* that only occurs on ungrazed low marshes (see box III).
- All lines of evidence support the **beneficial effects of short-term cessation of grazing for arthropod conservation**, and therefore rotational grazing. The duration of cessation may range between one and five years and on some places even longer without the encroachment of *E. atherica* (see Hamburger Hallig in Germany). Monitoring can show when plant species start decreasing in abundance, which is when grazing should be reinstated. It should be remembered when reinstating grazing, that the higher the stocking density, the more invertebrate species will disappear.
- **Grazing at intermediate stocking densities** (0.5 horse / 1 cow / 3–4 sheep ha^{-1}) will most likely create a heterogeneous sward and **benefit unpalatable plant species** such as J*uncus* spp., A*rtemisia maritima* and their associated insects.
- **Grazing at low stocking densities** (0.5 cow / 1–3 sheep ha^{-1}) will **be beneficial to palatable plant species** such as *A. tripolium* and many insect species, but will allow encroachment of *E. atherica* on the long term.

- **I recommend these last four types of management to be present at all times** to maximize the opportunities for coexistence of all targeted species, also those of which the ecological requirements and management effects are unknown. A shifting mosaic of management regimes over decade spanning periods should maximise conservation benefit.

FUTURE CHALLENGES

In the work presented I attempted to make a contribution to our understanding of the effects of large herbivores on arthropod communities. Still, many issues have remained unresolved, and new hypotheses have arisen.

First and foremost, only limited knowledge was gained on the long-term effects of different types of grazing management for arthropod communities. In order to design effective management strategies, it is imperative to understand the impact of the possible options over longer periods (> 10 years) and, preferably, large spatial scales. This is especially true for rotational grazing, of which we were only able to study two rotations.

Second, large groups of arthropods have not, or only to a limited extent, been assessed during this research. Not surprisingly, these are also the groups that were found to be under-represented in research in the literature study of chapter 2, such as aphids, flies and the hyper-diverse parasitic wasps. Not only are these groups important components of food webs due to their vast abundance and diversity, they also have significant agricultural importance as pests or bio-control agents and may be good predictors of overall arthropod species richness (Anderson et al. 2011). To include these groups will be a great future challenge.

Third, for only a small group of species suitable indicators have been established. The development of reliable indicators for other (groups of) species will aid the development of an effective monitoring of conservation success for arthropod communities, without having to depend on increasingly rare and highly burdened taxonomic experts. The list presented in box III can serve to generate meaningful indicators, but these will require validation in the field.

Fourth, perhaps the most important future challenge will be assessing habitat requirements of, and management impact on, salt-marsh specialist species that are, for as yet unknown reasons, rare. For example, the moths *Aristotelia brizella* and *Lobesia littoralis*, which feed on the not uncommon halophyte A*rmeria maritima*, but are rarely caught, or the ground beetle *Acupalpus elegans* and the braconid wasp *Chasmodon acares* of which neither habitat requirements nor prey species are known. It is these rare species that require our conservation efforts the most and still defy our understanding of their ecological requirements.

RELEVANCE FOR OTHER SYSTEMS

Grazing by livestock or (semi-)wild herbivores in natural, semi-natural or almost entirely artificial ecosystems is becoming increasingly common, with the spreading abandonment of agricultural lands and calls for rewilding (Donlan et al. 2006, Navarro and Pereira 2012). It is therefore imperative to understand the effects of grazing on all parts of the ecosystem.

Many of the results from this thesis will be relevant for other ecosystems as well, perhaps more so in productive than in unproductive systems. The meta-analysis presented in chapter 2 was compiled from a broad range of ecosystems, and the general framework presented there should apply to all systems. The negative relationship between large herbivore density and arthropod species richness seems to be general and not ecosystem specific (chapter 2) and only few studies have shown positive effects of grazing (Joern 2005, Vulliamy et al. 2006, Yoshihara et al. 2008, Woodcock and Pywell 2009). The key challenge here will be to understand under which conditions (ecosystem, productivity, herbivore density, etc.) positive effects of grazing on arthropod species richness can be found, and how this differs between different arthropod groups in relation to their life-history traits.

Apart from the general framework presented in chapter 2, several other hypotheses emerged from this work, which will be worthwhile testing in other ecosystems:

1) In chapter 4 evidence was presented that under intermediate herbivore densities, unpalatable plant species, in this case *Artemisia maritima* and the for sheep unpalatable *Juncus gerardii*, facilitated the establishment of grazing intolerant plant species, in a process known as associational resistance (Barbosa et al. 2009), and were responsible for the formation of grazed vegetation mosaics. This benefitted not only the specialised herbivorous invertebrates of these plants, but also many other arthropod species. Similar mosaics can be found on the salt marsh of Schiermonnikoog, where facilitation is provided by *J. maritimus* (pers obs), and other ecosystems (Olff et al. 1999). These observations suggest that arthropod communities can strongly benefit from facilitation between plant species, and it would be interesting to experimentally test this in other ecosystems.
2) Our results on soil compaction (chapter 5) are congruent with the predictions made by Schrama et al. (2013a, b) that soil compaction will be especially important on fine-textured clay soils, and less so on course soil types. Work in many more ecosystems is needed, though, to prove the generality of these predictions.
3) The importance of complex vegetation structure, as dealt with in all chapters of this thesis, is known to be of high importance in all systems (see chapter 2, Morris 2000). However, positive effects of a dense sward of grasses for arthropod species richness may be specific to flooding habitats, attenuating the effects of (tidal) inundations (chapter 3, chapter 4). In other, less productive but warmer ecosystems such as heathlands and calcareous grasslands, the dominance of mat-forming grasses may have detrimental effects on arthropod species richness, and in particular on thermophilic species. Understanding how dense vegetation affects arthropod communities in a variety of ecosystems that differ in productivity, temperature or environmental adversity, will aid in making evidence-based management decisions that consider the needs of arthropods.

EPILOGUE: The little things that run the world

In 1987, E.O. Wilson pleaded for the conservation of invertebrates in a seminal paper entitled "The little things that run the world". He argued that because of the myriad ecosystem processes performed by invertebrates, they deserve a better reputation as well as our conservation concern.

In this thesis, I showed that invertebrate communities are strongly, and often detrimentally, affected by large herbivores through competition, habitat modification and direct effects. In natural ecosystems, these large herbivores are, however, under strong top-down control of large carnivores, parodied as "The big things that run the world" (Terborgh 1988). The trophic cascades caused by the removal of top-carnivores, via large herbivores on invertebrate communities have rarely been investigated yet, but the first studies suggest strong positive effects of top-predators on invertebrate communities (Ripple and Beschta 2006, Terborgh and Feeley 2010), as well as amphibians (Ripple and Beschta 2006) and birds (Baril et al. 2011). Unfortunately, many large carnivore species have been eradicated from large parts of their former ranges, and are in immediate danger of extinction (Ripple et al. 2014), predicting a dark future for invertebrates.

Still, regardless of whether the big things or the little things run the world, it is the chemical processes performed by the microbes residing in the soil, water, air and in the guts of all animals that drive global biogeochemical cycles (Whitman et al. 1998). Hence, the little things running the world are a lot smaller than those targeted by E.O. Wilson. In the end, we are all merely vehicles for our gut microbes.

APPENDIX:
The fauna of the Noorderleech area

In prepraration for publication

These are the species found in the research area before and during the research period, using standardized trapping as described in this thesis, and numerous hand-catches. Species denoted bold only occur in saline habitats; * indicates species that probably do not reproduce in the study area.

ISOPODA
Matty P. Berg & Roel van klink
Philoscia moscorum
Porcellio scaber
Trachelipus rathkii

AMPHIPODA
Matty P. Berg
Ochtestia gammarellus

COLLEMBOLA
Matty P. Berg

Poduromorpha
Thalassaphorura debilis
Mesaphorura macrochaeta
Friesea truncata
Podura aquatica

Entomobryomorpha
Isotoma riparia
Isotoma palustris
Halisotoma maritima
Folsomia sexoculata
Isotomurus palustris
Lepidocyrtus violaceus

Symphypleona
Sminthurus viridis
Sminthurus nigromaculatus
Sphaeridia pumilis
Sminthurinus aureus

CHILOPODA
Matty P. Berg
Lamyctes emarginatus
Lithobius muticus/pelidnus

DIPLOPODA
Matty P. Berg
Brachydesmus superus
Polydesmus denticulatus

DERMAPTERA
Roel van Klink
Forficula auricularia

ORTHOPTERA
Roel van Klink
Conocephalus dorsalis

HEMIPTERA

Sternorrhyncha
Roel van Klink

TRIOZIDAE
Trioza chenopodii

Auchenorrhyncha
Roel van Klink

CIXIIDAE
*Tachycixius pilosus**

DELPHACIDAE
Prokelisia marginata
Chloriona glaucescens
Javesella pelucida
Javesella dubia

APHROPHORIDAE
Philaenus spumarius
Neophilaenus lineatus

CICADELLIDAE
Eupteryx artemisiae
Aphrodes aestuarina
Anoscopus limicola
Anoscopus serratulae
Macrosteles sordidipennis
Arthaldeus pascuellus
*Athysanus argentarius**
Conosanus obsoletus
Deltocephalus pulicaris
Errastunus occelaris
Euscelis lineolatus
Limotettix striola
Paramesus obtussifrons
*Psammotettix confinis**
Psammotettix putoni
Streptanus aemulans
Streptanus sordidus

Heteroptera
Berend Aukema, Philip Zijnstra, Roel van Klink, Maarten Schrama

CORIXIDAE
Callicorixa praeusta
Corixa affinis
Corixa panzeri
Corixa punctata
Hesperocorixa linnaei
Hesperocorixa sahlbergi
Paracorixa concinna
Sigara falleni
Sigara lateralis
Sigara limitata
Sigara stagnalis
Sigara striata

NAUCORIDAE
Ilyocoris cimicoides

NOTONECTIDAE
Notonecta glauca
Notonecta viridis

PLEIDAE
Plea minutisima

SALDIDAE
Chiloxanthus pilosus
Halosalda lateralis
Salda littoralis
Saldula pallipes
Saldula palustris
Saldula pilosella
Saldula arenicola

MIRIDAE
Apolygus lucorum
Capsus ater
Closterotomus norwegicus
Europiella artemisia
Europiella decolor
Harpocera thoracica
Liocoris tripustulatus
Lygus maritimus
Lygus rugulipennis
Orthotylus flavosparsus
Orthotylus moncreaffi
Orthotylus rubidus
Pithanus maerkelii
Trigonotylus caelestialium

LYGAEIDAE
Cymus claviculus

NABIDAE
Nabis lineatus

ANTHOCORIDAE
Anthocoris nemoralis
Anthocoris nemorum
Orius minutus
Orius niger

CERATOCOMBIDAE
Ceratocombus coleoptratus

LEPIDOPTERA

Maurice Jansen, Roel van Klink,
Corinna Rickert, Remco Hiemstra

BUCCULATRICIDAE
Bucculatrix maritima

COLEOPHORIDAE
Coleophora artemisiella
Coleophora asteris
Coleophora atriplicis
Coleophora deviella
Coleophora salicorniae

GELICHIIDAE
Scrobipalpa nitentella
Scrobipalpa salinella
Chrysoesthia sexguttella

GEOMETRIDAE
Eupithecia centaureata

HESPERIIDAE
Thymelicus lineola

NOCTUIDAE
Autographa gamma
Amphipoea oculea
Noctua pronuba

NYMPHALIDAE
Aglais urticae
*Aglais io**
*Coenonympha pamphilus**
Vanessa atalanta
*Vanessa cardui**

PIERIDAE
*Colias croceus**
*Pieris brassicae**
*Pieris napi**
*Pieris rapae**

PYRALIDAE
Ostrinia nubilalis

TORTRICIDAE
*Acleris comariana**
Clepsis spectrana
Eucosma tripoliana
Eucosma lacteana
Phalonidia affinitana
Phalonidia vectisana

COLEOPTERA

Oscar Vorst, Frank van Nunen,
Roel van Klink, Theodoor Heijerman,
Eric Bruning

GYRINIDAE
Gyrinus substriatus

HALIPLIDAE
Peltodytes caesus
Haliplus lineatocollis
Haliplus ruficollis
Haliplus fluviatilis
Haliplus immaculatus
Haliplus apicalis

NOTERIDAE
Noterus clavicornis

PAELOBIIDAE
Hygrobia hermanni

DYTISCIDAE
Laccophilus minutus
Hygrotus impressopunctatus
Hygrotus nigrolineatus
Hygrotus confluens
Hygrotus inaequalis
Hyphydrus ovatus
Hydroporus erythrocephalus
Hydroporus planus
Agabus conspersus
Ilybius subaeneus
Rhantus suturalis

CARABIDAE
Carabus granulatus
Nebria brevicollis
Notiophilus substriatus
Loricera pilicornis
Clivina fossor
Dyschirius salinus
Dyschirius tristis
Trechus quadristriatus
Bembidion properans
Bembidion varium
Bembidion semipunctatum
Bembidion assimile
Bembidion normannum
Bembidion minimum
Bembidion aeneum
Bembidion guttula
Bembidion lunulatum
Pogonus luridipennis
Pogonus chalceus
Poecilus cupreus
Pterostichus strenuus
Pterostichus diligens
Pterostichus vernalis
Pterostichus niger
Pterostichus melanarius
Agonum marginatum
Calathus melanocephalus
Amara plebeja
Amara communis
Amara aenea
Amara familiaris
Amara convexiuscula
Amara equestris
Anisodactylus binotatus
Harpalus rufipes
Harpalus affinis
Acupalpus elegans
Acupalpus meridianus
Dicheirotrichus gustavii
Badister bullatus
Badister sodalis

HYDROPHILIDAE
Helophorus rufipes
Helophorus aequalis
Helophorus brevipalpis
Helophorus obscurus
Helophorus fulgidicollis
Laccobius minutus
Helochares lividus
Enochrus bicolor
Hydrobius fuscipes
Hydrophilus piceus
Cercyon melanocephalus
Cercyon lateralis
Cercyon quisquilius
Cercyon pygmaeus
Cercyon tristis
Cercyon analis
Megasternum concinnum
Cryptopleurum minutum

HISTERIDAE
Margarinotus neglectus

HYDRAENIDAE
Ochthebius dilatatus
Ochthebius auriculatus
Ochthebius minimus
Ochthebius marinus

PTILIIDAE
Ptenidium fuscicorne
Acrotrichis grandicollis

LEIODIDAE
Choleva elongata
Sciodrepoides watsoni

SILPHIDAE
Thanatophilus sinuatus
Silpha tristis

STAPHYLINIDAE
Omalium rivulare
Lesteva longoelytrata
Amauronyx maerkelii
Brachygluta helferi
Mycetoporus punctus
Ischnosoma splendidum
Sepedophilus marshami
Tachyporus nitidulus
Tachyporus hypnorum
Tachyporus dispar
Tachyporus cf tersus
Tachyporus atriceps
Tachyporus pusillus

Tachinus rufipes
Aleochara lanuginosa
Tinotus morion
Oxypoda exoleta
Oxypoda brachyptera
Oxypoda haemorrhoa
Calodera aethiops
Gnypeta carbonaria
Gnypeta rubrior
Brundinia meridionalis
Brundinia marina
Aloconota gregaria
Geostiba circellaris
Philhygra elongatula
Philhygra palustris
Atheta laticollis
Atheta atramentaria
Atheta triangulum
Dinaraea angustula
Acrotona fungi
Acrotona amplicollis
Halobrecta flavipes
Amischa analis
Amischa nigrofusca
Amischa decipiens
Oligota pusillima
Oligota pumilio
Coprophilus striatulus
Carpelimus foveolatus
Carpelimus halophilus
Carpelimus pusillus
Bledius spectabilis
Bledius fergussoni
Oxytelus laqueatus
Anotylus insecatus
Anotylus rugosus
Anotylus sculpturatus
Anotylus tetracarinatus
Platystethus arenarius
Platystethus cornutus
Platystethus alutaceus
Platystethus nitens
Stenus comma
Stenus clavicornis
Stenus boops
Stenus melanopus
Stenus canaliculatus
Stenus brunnipes
Euaesthetus bipunctatus
Sunius bicolor
Lobrathium multipunctum
Lathrobium fulvipenne
Lathrobium longulum
Achenium depressum
Philonthus cognatus
Philonthus carbonarius
Philonthus varians
Philonthus quisquiliarius
Bisnius sordidus
Gabrius breviventer
Gabrius appendiculatus
Ocypus olens
Tasgius ater
Quedius simplicifrons
Quedius cf molochinus
Quedius semiaeneus
Gyrohypnus angustatus
Xantholinus longiventris

SCARABAEIDAE
Aphodius rufipes
Aphodius sphacelatus
Aphodius prodromus
Aphodius ater
Aphodius granarius

BYRRHIDAE
Byrrhus pilula

HETEROCERIDAE
Heterocerus fenestratus
Heterocerus hispidulus
Heterocerus maritimus

ELATERIDAE
Agriotes lineatus
Agriotes obscurus
Agriotes sputator

CANTHARIDAE
Cantharis fusca
Cantharis flavilabris
Cantharis lateralis
Cantharis rufa
Malthodes pumilus
Malthodes lobatus

KATERETIDAE
Brachypterus urticae
Brachypterus glaber

NITIDULIDAE
Meligethes aeneus
Meligethes nigrescens
Glischrochilus hortensis
Glischrochilus quadrisignatus

PHALACRIDAE
Stilbus testaceus

CRYPTOPHAGIDAE
Atomaria fuscata
Atomaria lewisi
Atomaria rhenana
Atomaria basalis
Atomaria scutellaris
Atomaria atricapilla
Atomaria testacea
Atomaria nigrirostris
Ephistemus globulus

COCCINELLIDAE
Coccidula rufa
Coccinella septempunctata
Coccinella undecimpunctata
Harmonia axyridis

LATRIDIIDAE
Enicmus transversus
Stephostethus lardarius
Corticaria impressa
Cortinicara gibbosa
Corticarina minuta

ANTHICIDAE
Omonadus floralis

CERAMBYCIDAE
Agapanthia villosoviridescens

CHRYSOMELIDAE
Donacia semicuprea
Cassida rubiginosa
Cassida vittata
Chrysolina staphylaea
Gastrophysa polygoni
Longitarsus plantagomaritimus
Longitarsus reichei
Longitarsus luridus
Lythraria salicariae
Neocrepidodera ferruginea
Chaetocnema concinna

BRENTIDAE
Ceratapion gibbirostre
Protapion assimile
Perapion hydrolapathi
Perapion marchicum
Apion frumentarium
Ischnopterapion virens

CURCULIONIDAE
Tanymecus palliatus
Sitona lepidus
Pelenomus zumpti
Rhinoncus inconspectus
Rhinoncus pericarpius
Amalus scortillum
Ceutorhynchus erysimi
Microplontus melanostigma
Hadroplontus litura
Trichosirocalus troglodytes
Mecinus collaris
Tournotaris bimaculata

NEUROPTERA

Roel van Klink
Chrysoperla carnea

HYMENOPTERA

TENTHREDINIDAE

Ad mol

Selandria melanosterna
Nematus myosotidis
Athalia rosae
Pachynematus clitellatus

DRYINIDAE

Roel van Klink

Gonathopus pedestris

FORMICIDAE

Kim Meijer

Lasius niger

APIDAE

Anne Jan Loonstra

Bombus lapidarius
Bombus campestris
Bombus terrestris
Apis mellifera

ICHNEUMONIDAE

Kees Zwakhals

Itoplectis maculator
Diplazon laetatorius
Schizopyga circulator

BRACONIDAE

Kees van Achterberg

Chasmodon acares

DIPTERA

CECIDOMYIIDAE

Roel van Klink

Cystiphora sonchi

STRATIOMYIDAE

Roel van Klink, Anne-Jan Loonstra

Chloromyia formosa
Nemotelus notatus
Nemotelus uliginosus
Microchrysa flavicornis

TEPHRITIDAE

Roel van Klink

Campiglossa plantaginis
Campiglossa absinthii

TABANIDAE

Roel van Klink

Chrysops relictus
Haematopota pluvialis

SYRPHIDAE

Anne Jan Loonstra, Roel van Klink, Remco Hiemstra

Dasysyrphus albostriatus
Episyrphus balteatus
Eristalinus aeneus
Eristalis intricaria
Eristalis tenax
Eristalis nemorum
Eupeodus corollae
Eupeodes luniger
Helophilus hybridus
Helophilus trivitattus
Lejops vittatus
Melanostoma mellinum
Platycheirus manicatus
Platycheirus peltatus
Pyrophaena granditarsa
Syrphus vitripennis

ARANEAE

Roel van Klink & Steven IJland

DICTYNIDAE

Argenna patula

CLUBIONIDAE

Clubiona stagnatilis
Clubiona phragmitis

LYCOSIDAE

Pardosa purbeckensis
Pardosa amentata
Pirata hygrophilus
Pirata piraticus
Trochosa ruricola

THERIDIIDAE

Enoplognatha mordax
Robertus arundineti
Robertus lividus

TETRAGNATHIDAE

Pachygnatha clercki
Pachygnatha degeeri

ARANAEIDAE

Larinioides cornutus
Araneus diadematus

LINYPHIIDAE

Agyneta decora
Allomengea scobigera
Baryphyma duffeyi
Bathyphantes approximatus
Bathyphantes gracilis
Centromerita bicolor
Centromerita concinna
Collinsia inerrans
Dicymbium nigrum
Erigone atra
Erigone dentipalpis
Erigone longipalpis
Gongylidiellum vivum
Hypomma bituberculatum
Leptorhoptrum rubustum
Micrargus subaequalis
Oedothorax apicatus
Oedothorax fuscus
Oedothorax retusus
Pelecopsis paralella
Pocadicnemis pumilla
Stemonyphantes lineatus
Tenuiphantes tenuis
Walckenaeria kochi

OPILIONES

Roel van Klink

Phalangium oplio
Oligolophus tridens

ACARI

Wim Dimmers & Roel van Klink

Mesostigmata

Geholaspis mandibularis
Cheiroseius salcorniae
Lasioseius confusus
Leioseius bicolor
Neojordensia laevis
Pachylaelaps siculus
Pergamasus crassipes
Pergamasus vagabundus
Hypoaspis aculeifer
Uropoda orbicularis

Oribatida

Liebstadia similis
Oribatella arctica litoralis
Ramusella insculpta

References

A

Abramoff, M. D., P. J. Magalhaes, and S. J. Ram. 2004. Image processing with ImageJ. Biophotonics International 11:36–52.

Adam, P. 1990. Saltmarsh ecology. Cambridge University Press, Cambridge.

Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479.

Agassiz, D. J. L. 2000. Lepidoptera of British saltmarshes. Pages 303–308 *in* B. R. Sherwood, B. E. Gardiner, and T. Harris, editors. British Saltmarshes. Linnean Society of London, London.

Allan, E., and M. J. Crawley. 2011. Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. Ecology letters 14:1246–53.

Alterra. 2013. Begrazing in Nederland. http://www.synbiosys.alterra.nl/begrazing/.

Anderson, A., S. McCormack, A. Helden, H. Sheridan, A. Kinsella, and G. Purvis. 2011. The potential of parasitoid Hymenoptera as bioindicators of arthropod diversity in agricultural grasslands. Journal of Applied Ecology 48:382–390.

Andresen, H., J. P. Bakker, M. Brongers, B. Heydemann, and U. Irmler. 1990. Long-term changes of salt marsh communities by cattle grazing. Vegetatio 89:137–148.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO2? Climatic Change 29:91–99.

Aritajat, U., D. S. Madge, and P. T. Gooderham. 1977. Effects of compaction of agricultural soils on soil fauna .1. Field investigations. Pedobiologia 17:262–282.

Armstrong, W., E. J. Wright, S. Lythe, and T. J. Gaynard. 1985. Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt-marsh. Journal of Ecology 73:323–339.

Atkinson, P. W., D. Buckingham, and A. J. Morris. 2004. What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? Ibis 146:99–107.

Atkinson, P. W., R. J. Fuller, J. A. Vickery, G. J. Conway, J. R. B. Tallowin, R. E. N. Smith, K. A. Haysom, T. C. Ings, E. J. Asteraki, and V. K. Brown. 2005. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. Journal of Applied Ecology 42:932–942.

Aukema, B., and C. Rieger. 1995-2006. Catalogue of the Heteroptera of the Palearctic region 1-6. Nederlandse Entomologische Vereniging, Amsterdam.

Awmack, C. S., and S. R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. Annual review of entomology 47:817–44.

B

Bacaro, G., M. Gioria, and C. Ricotta. 2011. Testing for differences in beta diversity from plot-to-plot dissimilarities. Ecological Research 27:285–292.

Bacaro, G., M. Gioria, and C. Ricotta. 2013. Beta diversity reconsidered. Ecological Research 28:537–540.

Bailey, J. K., and T. G. Whitham. 2006. Interactions between cottonwood and beavers positively affect sawfly abundance. Ecological Entomology 31:294–297.

Bakker, E. S., H. Olff, and J. M. Gleichman. 2009. Contrasting effects of large herbivore grazing on smaller herbivores. Basic and Applied Ecology 10:141–150.

Bakker, E. S., H. Olff, C. Vandenberghe, K. De Maeyer, R. Smit, J. M. Gleichman, and F. W. M. Vera. 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. Journal of Applied Ecology 41:571–582.

Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecology Letters 9:780–788.

Bakker, J. P. 1978. Changes in a salt-marsh vegetation as a result of grazing and mowing - A 5-year study of permanent plots. Vegetatio 38:77–87.

Bakker, J. P. 1985. The impact of grazing on plant-communities, plant-populations and soil-conditions on salt marshes. Vegetatio 62:391–398.

Bakker, J. P. 1989. Nature management by cutting and grazing. Kluwer Academic Publishers, Dordrecht.

Bakker, J. P., D. Bos, and Y. De Vries. 2003. To graze or not to graze: that is the question. Pages 67–88 *in* W. J. Wolff, K. Essink, A. Kellermann, and M. A. Van Leeuwe, editors. Proceedings 10th International Scientific Wadden Sea Symposium. Ministry of Agriculture, Nature Management and Fisheries and Department of Marine Biology, University of Groningen, Groningen.

Bakker, J. P., J. Deleeuw, K. S. Dijkema, P. C. Leendertse, H. H. T. Prins, and J. Rozema. 1993. Salt marshes along the coast of the Netherlands. Hydrobiologia 265:73–95.

Bakker, J. P., M. Dijkstra, and P. T. Russchen. 1985. Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh gradient. New Phytologist 101:291–308.

Bakker, J. P., L. Gálvez Bravo, and A. M. Mouissie. 2008. Dispersal by cattle of salt-marsh and dune species into salt-marsh and dune communities. Plant Ecology 197:43–54.

Bakker, J. P., J. De Leeuw, and S. E. Van Wieren. 1984. Micro-patterns in grassland vegetation created and sustained by sheep-grazing. Vegetatio 55:153–161.

Báldi, A., P. Batáry, and D. Kleijn. 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary – analysing assemblages of 1200 species. Agriculture, Ecosystems & Environment 166:28–34.

Balmer, O., and A. Erhardt. 2000. Consequences of succession on extensively grazed grasslands for central European butterfly communities: Rethinking conservation practices. Conservation Biology 14:746–757.

Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annual Review of Ecology, Evolution, and Systematics 40:1–20.

Bardgett, R. D., J. C. Frankland, and J. B. Whittaker. 1993. The effects of agricultural management on the soil biota of some upland grasslands. Agriculture Ecosystems & Environment 45:25–45.

Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84:2258–2268.

Baril, L. M., A. J. Hansen, R. Renkin, and R. Lawrence. 2011. Songbird response to increased willow (*Salix* spp.) growth in Yellowstone's northern range. Ecological Applications 21:2283–2296.

Barker, G. 1985. Prehistoric farming in Europe. Cambridge University Press, Cambridge.

Barton, K. 2013. MuMIn: Multi-model inference. R package version 1.9.11.

Barton, P. S., S. A. Cunningham, D. B. Lindenmayer, and A. D. Manning. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171:761–72.

Batáry, P., A. Báldi, M. Sárospataki, F. Kohler, J. Verhulst, E. Knop, F. Herzog, and D. Kleijn. 2010. Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. Agriculture Ecosystems & Environment 136:35–39.

Bates, D., M. Maechler, and B. Bolker. 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.

Bayfield, N. 1979. Some effects of trampling on *Molophilus ater* (Meigen) (Diptera, Tipulidae). Biological Conservation 16:219–232.

Bazelmans, J., D. Meier, A. Nieuwhof, T. Spek, and P. Vos. 2012. Understanding the cultural historical value of the Wadden Sea region. The co-evolution of environment and society in the Wadden Sea area in the Holocene up until early modern times (11,700 BC–1800 AD): An outline. Ocean & Coastal Management 68:114–126.

Beck, J., J. D. Holloway, and W. Schwanghart. 2013. Undersampling and the measurement of beta diversity. Methods in Ecology and Evolution 4:370–382.

Beeftink, W. G. 1977. The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. Pages 109–155 *in* V. J. Chapman, editor. Ecosystems of the World 1: Wet Coastal Ecosystems. Elsevier, Amsterdam.

Bell, J. R., D. A. Bohan, E. M. Shaw, and G. S. Weyman. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bulletin of entomological research 95:69–114.

Bell, J. R., C. P. Wheater, and W. R. Cullen. 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. Journal of zoology 255:377–387.

Belovsky, G. E., J. B. Slade, and B. A. Stockhoff. 1990. Susceptibility to predation for different grasshoppers - an experimental-study. Ecology 71:624–634.

Ben-Ari, M., and M. Inbar. 2013. When herbivores eat predators: predatory insects effectively avoid incidental ingestion by mammalian herbivores. PloS one 8:e56748.

Benton, T. G., D. M. Bryant, L. Cole, and H. Q. P. Crick. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology 39:673–687.

Berg, G., P. Esselink, M. Groeneweg, and K. Kiehl. 1997. Micropatterns in *Festuca rubra*-dominated salt-marsh vegetation induced by sheep grazing. Plant Ecology 132:1–14.

Berggren, Å. 2004. Impact of grazing on individual male movement in Roesel's Bush-Cricket *Metrioptera roeseli*: one possible clue to species range expansion. Journal of Insect Behavior 17:419–429.

Bestelmeyer, B. T., and J. A. Wiens. 2001. Ant biodiversity in semiarid landscape mosaics: The consequences of grazing vs. natural heterogeneity. Ecological Applications 11:1123–1140.

Bethge, W. 1973. Ökologisch-physiologische Untersuchungen über die Bindung von *Erigone Longipalpis* (Araneae, Micryphantidae) an das Litoral. Faunistisch-Ökologische Mitteilungen 4:223–240.

Beylich, A., H.-R. Oberholzer, S. Schrader, H. Hoeper, and B.-M. Wilke. 2010. Evaluation of soil compaction effects on soil biota and soil biological processes in soils. Soil & Tillage Research 109:133–143.

Beynon, S. A., M. Peck, D. J. Mann, and O. T. Lewis. 2012. Consequences of alternative and conventional endoparasite control in cattle for dung-associated invertebrates and ecosystem functioning. Agriculture Ecosystems & Environment 162:36–44.

Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemuller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, W. E. Kunin, and R. Ohlemüller. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? The American naturalist 180:407–24.

Bockelmann, A. C., and R. Neuhaus. 1999. Competitive exclusion of *Elymus athericus* from a high-stress habitat in a European salt marsh. Journal of Ecology 87:503–513.

Boeken, M., K. Desender, B. Drost, T. van Gijzen, B. Koese, J. Muilwijk, R. Vermeulen, and H. Turin. 2002. De Loopkevers van Nederland en Vlaanderen (Coleoptera: Carabidae). Jeugdbondsuitgeverij, Nederland.

Boele, A., J. Van Bruggen, A. Van Dijk, F. Hustings, J.-W. Vergeer, and C. Plate. 2013. Broedvogels in Nederland in 2011. Sovon rapport 2013/01. Nijmegen.

Bogich, T. L., G. M. Barker, K. Mahlfeld, F. Climo, R. Green, and A. Balmford. 2012. Fragmentation, grazing and the species – area relationship. Ecography 35:224–231.

Bonal, R., and A. Munoz. 2007. Multi-trophic effects of ungulate intraguild predation on acorn weevils. Oecologia 152:533–540.

Bonte, D., B. Bossuyt, and L. Lens. 2007. Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. Behavioral Ecology 18:438–443.

Bonte, D., and D. Maes. 2008. Trampling affects the distribution of specialised coastal dune arthropods. Basic and Applied Ecology 9:726–734.

Bonte, D., N. Vandenbroecke, L. Lens, and J.-P. Maelfait. 2003. Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. Proceedings of the Royal Society B-Biological Sciences. 270: 1601–1607.

Bos, D., M. Loonen, M. Stock, F. Hofeditz, S. Van Der Graaf, and J. P. Bakker. 2005. Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing. Journal for Nature Conservation 15:1–15.

Bouchard, V., M. Tessier, F. Digaire, J. P. Vivier, L. Valery, J. C. Gloaguen, and J. C. Lefeuvre. 2003. Sheep grazing as management tool in Western European saltmarshes. Comptes Rendus Biologies 326:S148–S157.

Bourn, N. A., and J. A. Thomas. 2002. The challenge of conserving grassland insects at the margins of their range in Europe. Biological Conservation 104:285–292.

Bowdish, T. I., and P. Stiling. 1998. The influence of salt and nitrogen on herbivore abundance: direct and indirect effects. Oecologia 113:400–405.

Brook, A. J., B. A. Woodcock, M. Sinka, and A. J. Vanbergen. 2008. Experimental verification of suction sampler capture efficiency in grasslands of differing vegetation height and structure. Journal of Applied Ecology 45:1357–1363.

Butenschoen, O., S. Marhan, and S. Scheu. 2008. Response of soil microorganisms and endogeic earthworms to cutting of grassland plants in a laboratory experiment. Applied Soil Ecology 38:152–160.

Butler, S. J., and S. Gillings. 2004. Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. Ibis 146:123–130.

C

Calderone, N. W. 2012. Insect pollinated crops, insect pollinators and US agriculture: trend analysis of aggregate data for the period 1992-2009. PloS one 7:e37235.

Campbell, K., and M. Borner. 1995. Population trends and distribution of Serengeti herbivores: Implications for management. Pages 117–145 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II Dynamics, Management, and Conservation of an Ecosystem. University of Chicago Press, Chicago and London.

Cardoso, P., T. L. Erwin, P. a. V. Borges, and T. R. New. 2011. The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation 144:2647–2655.

Caruso, T., M. Taormina, and M. Migliorini. 2012. Relative role of deterministic and stochastic determinants of soil animal community: a spatially explicit analysis of oribatid mites. Journal of Animal Ecology 81:214–221.

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation 103:33–49.

Chambers, R. J. 1986. Preliminary experiments on the potential of hoverflies [Dipt.: Syrphidae] for the control of aphids under glass. Entomophaga 31:197–204.

Chaneton, E. J., and R. S. Lavado. 1996. Soil nutrients and salinity after long-term grazing exclusion in a flooding pampa grassland. Journal of Range Management 49:182.

Chappell, H. G., J. F. Ainsworth, R. A. D. Cameron, and M. Redfern. 1971. The effect of trampling on a chalk grassland ecosystem. Journal of Applied Ecology 8:869–882.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences 104:17430–17434.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. Science 328:1388–1391.

Chase, J. M., E. G. Biro, W. A. Ryberg, and K. G. Smith. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. Ecology Letters 12:1210–1218.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: Linking classical and contemporary approaches. University of Chicago Press, Chicago and London.

Cheng, L. 1976. Marine Insects.North Holland publishing, Amsterdam / Oxford.

Cherrett, J. M. 1964. The distribution of spiders on the Moor House National Nature Reserve, Westmorland. Journal of Animal Ecology 33:27–48.

Cherrill, A. J., and V. K. Brown. 1992. Ontogenic changes in the microhabitat preferences of *Decticus verrucivorus* (Orthoptera, Tettigoniidae) at the edge of its range. Ecography 15:37–44.

Clausen, H. D., H. B. Holbeck, and J. Reddersen. 2001. Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. Biological Conservation 98:167–178.

Clements, F. E. 1916. Plant succession – An analysis of the development of vegetation. Carnegie institute of Washington, Washington.

Cobben, R. H. 1960. Die Uferwanzen Europas. Pages 209–263 *in* W. Stichel, editor. Illustrierte Bestimmungstabellen der Wanzen. II Europa. Berlin: Hermsdorf, Berlin.

Cole, L., S. M. Buckland, and R. D. Bardgett. 2008. Influence of disturbance and nitrogen addition on plant and soil animal diversity in grassland. Soil Biology & Biochemistry 40:505–514.

Cole, L. J., M. L. Pollock, D. Robertson, J. P. Holland, D. I. McCracken, and W. Harrison. 2010. The influence of fine-scale habitat heterogeneity on invertebrate assemblage structure in upland semi-natural grassland. Agriculture Ecosystems & Environment 136:69–80.

Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64:87–94.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Cumming, D. H. M., and G. S. Cumming. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. Oecologia 134:560–568.

Curry, J. P. 1976. Some effects of animal manures on earthworms in grassland. Pedobiologia 16:425–438.

D

Dauber, J., T. Purtauf, A. Allspach, J. Frisch, K. Voigtländer, and V. Wolters. 2005. Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. Global Ecology and Biogeography 14:213–221.

Davy, A. J., M. J. H. Brown, H. L. Mossman, and A. Grant. 2011. Colonization of a newly developing salt marsh: disentangling independent effects of elevation and redox potential on halophytes. Journal of Ecology 99:1350–1357.

Day, T. A., and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180–188.

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

Dennis, P., M. B. Thomas, and N. W. Sotherton. 1994. Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. Journal of Applied Ecology 31:361–370.

Dennis, P., M. R. Young, and C. Bentley. 2001. The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. Agriculture Ecosystems & Environment 86:39–57.

Dennis, P., M. R. Young, and I. J. Gordon. 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23:253–264.

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

Denno, R. E., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Dobel, M. D. Eubanks, J. E. Losey, and G. A. Langellotto. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. Ecological Monographs 66:389–408.

Denno, R. F. 1980. Ecotope differentiation in a guild of sap-feeding insects on the salt-marsh grass, *Spartina patens*. Ecology 61:702–714.

Denno, R. F. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. Annual Review of Entomology 40:297–331.

Desender, K., T. Backeljau, K. Delahaye, and L. De Meester. 1998. Age and size of European saltmarshes and the population genetic consequences for ground beetles. Oecologia 114:503–513.

Desender, K., and J. P. Maelfait. 1999. Diversity and conservation of terrestrial arthropods in tidal marshes along the River Schelde: a gradient analysis. Biological Conservation 87:221–229.

Devereux, C. L., C. U. Mckeever, T. G. Benton, and M. J. Whittingham. 2004. The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats. Ibis 146:115–122.

De Deyn, G. B., C. E. Raaijmakers, H. R. Zoomer, M. P. Berg, P. C. de Ruiter, H. A. Verhoef, T. M. Bezemer, and W. H. van der Putten. 2003. Soil invertebrate fauna enhances grassland succession and diversity. Nature 422:711–713.

Dhuyvetter, H., F. Hendrickx, E. Gaublomme, and K. Desender. 2007. Differentiation between two salt marsh beetle ecotypes: Evidence for ongoing speciation. Evolution 61:184–193.

Di, H. J., K. C. Cameron, J. Milne, J. J. Drewry, N. P. Smith, T. Hendry, S. Moore, and B. Reijnen. 2001. A mechanical hoof for simulating animal treading under controlled conditions. New Zealand Journal of Agricultural Research 44:111–116.

Dierßen, K., I. Eischeid, S. Gettner, U. Hamann, K. Kiehl, J. Walter, T. Tischler, A. Mieth, H. Meyer, H. D. Reinke, I. Tutlowitzki, H. Fock, and A. Haase. 1994. Ökosystemforschung Wattenmeer Schleswig-Holstein - Teilvorhaben A 5.2 und A5.3. Bioindikatoren im Supralitoral. Teilbericht A: Die Beweidungsexperimente im Sönke-Nissen-Koog- und Friedrichskoog- Vorland. . Kiel.

Donlan, J. C., J. Berger, C. E. Bock, J. H. Bock, D. A. Burney, J. A. Estes, D. Foreman, P. S. Martin, G. W. Roemer, F. a Smith, M. E. Soulé, and H. W. Greene. 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. The American naturalist 168:660–681.

Douglas, D. J. T., D. M. Evans, and S. M. Redpath. 2008. Selection of foraging habitat and nestling diet by Meadow Pipits *Anthus pratensis* breeding on intensively grazed moorland. Bird Study 55:290–296.

Duelli, P., and M. K. Obrist. 1998. In search of the best correlates for local organismal biodiversity in cultivated areas. Biodiversity & Conservation 7:297–309.

Duffey, E. 1962. A Population Study of Spiders in Limestone Grassland - Field-Layer Fauna. Oikos 13:15–34.

Duffey, E. 1975. The effects of human trampling on the fauna of grassland litter. Biological Conservation 7:255–274.

Dumont, B., N. Rossignol, G. Loucougaray, P. Carrère, J. Chadoeuf, G. Fleurance, A. Bonis, A. Farruggia, S. Gaucherand, C. Ginanea, F. Louault, B. Marion, F. Mesléard, and N. Yavercovski. 2012. When does grazing generate stable vegetation patterns in temperate pastures? Agriculture, Ecosystems, & Environment 153:50–56.

Dunn, R. R. 2005. Modern insect extinctions, the neglected majority. Conservation Biology 19:1030–1036.

Dunn, R. R., N. C. Harris, R. K. Colwell, L. P. Koh, and N. S. Sodhi. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? Proceedings of the Royal Society B-Biological Sciences 276:3037–45.

E

Ebeling, A., A.-M. Klein, W. W. Weisser, and T. Tscharntke. 2012. Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. Oecologia 169:453–465.

EEA (European Environmental Agency). 2004. High nature value farmland. Characteristics, trends and policy challenges. EEA Report No1/2004. Copenhagen.

Eilers, S., L. B. Pettersson, and E. Öckinger. 2013. Micro-climate determines oviposition site selection and abundance in the butterfly *Pyrgus armoricanus* at its northern range margin. Ecological Entomology 38:183–192.

Ellwood, M. D. F., A. Manica, and W. A. Foster. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. Ecology Letters 12:277–284.

Escobar, F., G. Halffter, and L. Arellano. 2007. From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. Ecography 30:193–208.

Esselink, P., L. F. M. Fresco, and K. S. Dijkema. 2002. Vegetation change in a man-made salt marsh affected by a reduction in both grazing and drainage. Applied Vegetation Science 5:17–32.

Esselink, P., J. Petersen, S. Arens, J. P. Bakker, J. Bunje, K. S. Dijkema, N. Hecker, A. V. Hellwig, B. Jensen, B. Kers, P. Körber, E. J. Lammerts, G. Lüerssen, M. Vreeken, H. Marencic, M. Stock, R. M. Veeneklaas, and M. Wolters. 2009. Salt Marshes. Thematic Report No. 8. *in* H. Marencic and J. De Vlas, editors. Quality Status Report 2009. WaddenSea Ecosystem No. 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.

Esselink, P., W. Zijlstra, K. S. Dijkema, and R. van Diggelen. 2000. The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. Biological Conservation 93:61–76.

Evans, D. M., S. M. Redpath, and S. A. Evans. 2005. Seasonal patterns in the productivity of Meadow Pipits in the uplands of Scotland. Journal of Field Ornithology 76:245–251.

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

F

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics 34:487–515.

FAO (Food and Agriculture organisation of the United Nations). 2008. Are grasslands under threat? Brief analysis of FAO statistical data on pasture and fodder crops. http://www.fao.org/uploads/media/ grass_stats_1.pdf.

Farruggia, A., B. Dumont, A. Scohier, T. Leroy, P. Pradel, and J.-P.-P. Garel. 2012. An alternative rotational stocking management designed to favour butterflies in permanent grasslands. Grass and Forage Science 67:136–149.

Fattorini, S., R. L. H. Dennis, and L. M. Cook. 2011. Conserving organisms over large regions requires multi-taxa indicators: One taxon's diversity-vacant area is another taxon's diversity zone. Biological Conservation 144:1690–1701.

Finch, O. D., H. Krummen, F. Plaisier, and W. Schultz. 2007. Zonation of spiders (Araneae) and carabid beetles (Coleoptera : Carabidae) in island salt marshes at the North Sea coast. Wetlands Ecology and Management 15:207–228.

Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature 429:407–10.

Fisher, A. R. A., A. S. Corbet, and C. B. Williams. 1943. The number of animals in a random sample of an animal population. Journal of Animal Ecology 12:42–58.

Fisher Barham, D., and A. J. A. Stewart. 2005. Differential indirect effects of excluding livestock and rabbits from chalk heath on the associated leafhopper (Hemiptera: Auchenorrhyncha) fauna. Journal of Insect Conservation 9:351–361.

Fjellberg, A. 1998. The Collembola of Fennoscandia and Denmark part I: Poduromorpha. . Brill, Leiden.

Fjellberg, A. 2007. The Collembola of Fennoscandia and Denmark part II: Entomobryomorpha and Symphypleona. . Brill, Leiden.

Fleishman, E., and D. D. Murphy. 2009. A realistic assessment of the indicator potential of butterflies and other charismatic taxonomic groups. Conservation biology 23:1109–16.

Forbes, G. S., J. W. Van Zee, W. Smith, and W. G. Whitford. 2005. Desert grassland canopy arthropod species richness: temporal patterns and effects of intense, short-duration livestock grazing. Journal of Arid Environments 60:627–646.

Ford, H., A. Garbutt, L. Jones, and D. L. Jones. 2012. Methane, carbon dioxide and nitrous oxide fluxes from a temperate salt marsh: Grazing management does not alter global warming potential. Estuarine Coastal and Shelf Science 113:182–191.

Ford, H., A. Garbutt, L. Jones, and D. L. Jones. 2013. Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. Insect Conservation and Diversity 6:189–200.

Foster, W. A., and J. E. Treherne. 1976. Effects of tidal submergence on an intertidal aphid, *Pemphigus trehernei* Foster. Journal of Animal Ecology 45:291–301.

Franzen, M., and S. G. Nilsson. 2008. How can we preserve and restore species richness of pollinating insects on agricultural land? Ecography 31:698–708.

Freude, H., K. W. Harde, G. A. Lohse, and B. (eds) Klausnitzer. (1965–1999). Die Käfer Mitteleuropas bd 1-15. Goecke & Everts, Krefeld.

Freymann, B. P., R. Buitenwerf, O. Desouza, and H. Olff. 2008. The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review. European Journal of Entomology 105:165–173.

Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237–241.

Fuentes, E. R., and F. M. Jaksic. 1988. The hump-backed species-diversity curve - Why has it not been found among land animals. Oikos 53:139–143.

Fuller, R. J., and S. J. Gough. 1999. Changes in sheep numbers in Britain: implications for bird populations. Biological Conservation 91:73–89.

G

Gardner, S. M. M., S. E. E. Hartley, A. Davies, and S. C. F. Palmer. 1997. Carabid communities on heather moorlands in northeast Scotland: The consequences of grazing pressure for community diversity. Biological Conservation 81:275–286.

Georges, A., P. Fouillet, and J. Pétillon. 2011. Changes in salt-marsh carabid assemblages after an invasion by the native grass *Elymus athericus*. Pages 407–420 *in* D. J. Kotze, T. Assmann, J. Noordijk, H. Turin, and R. Vermeulen, editors. Carabid beetles as bioindicators: Biogeographical, ecological and environmental studies. Proceedings of the XIV European Carabidologists MeetingZookeys 10. Pensoft publishers, Sofia, Moscow.

Gibson, C. W. D., V. K. Brown, L. Losito, and G. C. McGavin. 1992a. The response of invertebrate assemblies to grazing. Ecography 15:166–176.

Gibson, C. W. D., C. Hambler, and V. K. Brown. 1992b. Changes in spider (Araneae) assemblages in relation to succession and grazing management. Journal of Applied Ecology 29:132–142.

Gish, M., A. Dafni, and M. Inbar. 2010. Mammalian herbivore breath alerts aphids to flee host plant. Current Biology 20:628–629.

Gomez, J. M. 2003. Herbivory reduces the strength of pollinator-mediated selection in the Mediterranean herb *Erysimum mediohispanicum*: Consequences for plant specialization. American Naturalist 162:242–256.

Gómez, J. M., and A. González-Megías. 2002. Asymmetrical interactions between ungulates and phytophagous insects: Being different matters. Ecology 83:203–211.

Gómez, J. M., and A. González-Megías. 2007. Long-term effects of ungulates on phytophagous insects. Ecological Entomology 32:229–234.

Goulet, H. 2003. Biodiversity of ground beetles (Coleoptera : Carabidae) in Canadian agricultural soils. Canadian journal of soil science 83:259–264.

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

Gwynne, M. D., and R. H. V. Bell. 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature 220:390–393.

H

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029–1039.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. The American naturalist 158:17–35.

Hågvar, S., O. Glesne, and E. Østbye. 2011. Food habits and niche overlap in three alpine passerine birds, South Norway. Ornis Norvegica 32:56–73.

Hamilton, A. J., Y. Basset, K. K. Benke, P. S. Grimbacher, S. E. Miller, V. Novotn_, G. A. Samuelson, N. E. Stork, G. D. Weiblen, and J. D. L. Yen. 2010. Quantifying uncertainty in estimation of tropical arthropod species richness. The American naturalist 176:90–5.

Hamilton, E. W., and D. A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tollerant grass. Ecology 82:2397–2402.

Hamza, M. A., and W. K. Anderson. 2005. Soil compaction in cropping systems - A review of the nature, causes and possible solutions. Soil & Tillage Research 82:121–145.

Hänggi, A., E. Stöckli, and W. Nentwig. 1995. Habitats of Central European spiders. Centre Suisse de cartoghraphie de la faune, Neuchatel.

Harvey, P. R., D. R. Nellist, and M. G. Telfer. 2002. Provisional atlas of British spiders (Arachnida, Araneae), Volumes 1 & 2. Biological records centre, Huntingdon.

Hedges, L. V, J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Heisler, C. 1994. Effects of soil compaction on soil mesofauna (Collembola and Gamasina) - a 3-year field-study. Pedobiologia 38:566–576.

Helden, A. J., A. Anderson, H. Sheridan, and G. Purvis. 2010. The role of grassland sward islets in the distribution of arthropods in cattle pastures. Insect Conservation and Diversity 3:291–301.

Hemminga, M. A., and J. Van Soelen. 1988. Estuarine gradients and the growth and development of *Agapanthia villosoviridescens*, (Coleoptera), a stem-borer of the salt marsh halophyte *Aster tripolium*. Oecologia 77:307–312.

Hemminga, M. A., and J. Van Soelen. 1992. The performance of the leaf mining Microlepidopteran *Bucculatrix maritima* (Stt) on the salt-marsh halophyte, *Aster tripolium* (L), exposed to different salinity conditions. Oecologia 77:422–427.

Heydemann, B. 1960. Die biozönotische Entwicklung vom Vorland zum Koog. 1. Teil: Spinnen (Araneae). Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur in Mainz 11:474–770.

Heydemann, B. 1962. Die biozönotische Entwicklung vom Vorland zum Koog. 2. Teil: Käfer (Coleoptera). Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur in Mainz. 11:771–964.

Heydemann, B. 1979. Responses of animals to spatial and temporal environmental hereogeneity within salt marshes. Pages 145–163 *in* R. L. Jefferies and D. J. de Jong, editors. Ecological processes in coastal environments. Blackwell scientific publications, Oxford.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Hobbs, N. T. 2006. Large herbivores as sources of disturbance in ecosystems. Pages 261–288 in K. Danell, R. Bergstrom, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge university press, Cambridge.

Hobbs, N. T., and D. M. Swift. 1988. Grazing in herds - when are nutritional benefits realized. American Naturalist 131:760–764.

Hobbs, R. J. 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. Conservation Biology 15:1522–1528.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324–337.

Hofmann, T. A., and C. F. Mason. 2006. Importance of management on the distribution and abundance of Staphylinidae (Insecta : Coleoptera) on coastal grazing marshes. Agriculture Ecosystems & Environment 114:397–406.

Holland, J. N., W. Cheng, and D. A. Crossley. 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. Oecologia 107:87–94.

Holmes, C. W. 1974. The Massey grass meter. Dairy Farmer Annual. Massey University, Palmerston North.

Horn, R., H. Domzal, A. Slowinskajurkiewicz, and C. Vanouwerkerk. 1995. Soil compaction processes and their effects on the structure of arable soils and the environment. Soil & Tillage Research 35:23–36.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346.

Hughes, A. M. 1976. The mites of stored food and houses. Ministry of Agriculture, Fisheries and Food, Great Britain.

Humbert, J.-Y., J. Ghazoul, and T. Walter. 2009. Meadow harvesting techniques and their impacts on field fauna. Agriculture, Ecosystems & Environment 130:1–8.

Hutchinson, K. J., and K. L. King. 1980. The effects of sheep stocking level on invertebrate abundance, biomass and energy-utilization in a temperate, sown grassland. Journal of Applied Ecology 17:369–387.

Hylander, K., and J. Ehrlén. 2013. The mechanisms causing extinction debts. Trends in Ecology & Evolution 28:341–346.

I

Irmler, U., K. Heller, H. Meyer, and H. D. Reinke. 2002. Zonation of ground beetles (Coleoptera_: Carabidae) and spiders (Araneida) in salt marshes at the North and the Baltic Sea and the impact of the predicted sea level increase. Biodiversity and Conservation 11:1129–1147.

Irmler, U., and B. Heydemann. 1985. Effects of cattle grazing on cicad populations in salt-meadows on Northern Germany. Mittleilungen der deutschen Gesellschaft für allgemeine und angewandte Entomologie 4:264–267.

Irmler, U., and B. Heydemann. 1986. Die ökologische Problematik de Beweidung von Salzwiesen an der Niedersächsischen Küste - am beispiel der Leybucht. Niedersächsisches Landesverwaltungsamt, Fachbehörde für Naturschutz, Hannover.

J

Jankielsohn, A., C. H. Scholtz, and S. V Louw. 2001. Effect of habitat transformation on dung beetle assemblages: A comparison between a South African nature reserve and neighboring farms. Environmental Entomology 30:474–483.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48:215–267.

Jáuregui, B. M., R. Rosa-García, U. Garcia, M. F. Wallisdevries, K. Osoro, R. Celaya, and R. Rosagarcia. 2008. Effects of stocking density and breed of goats on vegetation and grasshopper occurrence in heathlands. Agriculture Ecosystems & Environment 123:219–224.

Jay-Robert, P., J. Niogret, F. Errouissi, M. Labarussias, E. Paoletti, M. V. Luis, and J.-P. Lumaret. 2008. Relative efficiency of extensive grazing vs. wild ungulates management for dung beetle conservation in a heterogeneous landscape from Southern Europe (Scarabaeinae, Aphodiinae, Geotrupinae). Biological Conservation 141:2879–2887.

Jensen, P., G. L. Jacobson, and D. E. Willard. 1973. Effects of mowing and raking on Collembola. Ecology 54:564–572.

Joern, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. Ecology 86:861–873.

Joern, A., and L. R. Lawlor. 1981. Guild structure in grasshopper assemblages based on food and microhabitat resources. Oikos 37:93–104.

Joern, A., and A. N. Laws. 2013. Ecological mechanisms underlying arthropod diversity in grasslands. Annual Reviews of Entomology 58:19–36.

K

Kacelnik, A. 1984. Central place foraging in starlings (*Sturnus vulgaris*) .1. patch residence time. Journal of Animal Ecology 53:283–299.

Kaplan, I., and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. Ecology Letters 10:977–994.

Karg, W. 1993. Acari (Acarina), Milben Parasitiformes (Anactinotrichaeta) Cohors Gamasina Leach. Raubmilben. Gustav Fischer Verlag, New York.

Keesing, F., B. F. Allan, T. P. Young, and R. S. Ostfeld. 2013. Effects of wildlife and cattle on tick abundance in central Kenya. Ecological Applications 23:1410–1418.

Kiehl, K., I. Eischeid, S. Gettner, and J. Walter. 1996. Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. Journal of Vegetation Science 7:99–106.

Kiehl, K., P. Esselink, S. Gettner, and J. P. Bakker. 2001. The impact of sheep grazing on net nitrogen mineralization rate in two temperate salt marshes. Plant Biology 3:553–560.

King, K. L., and K. J. Hutchinson. 1976. Effects of sheep stocking intensity on abundance and distribution of mesofauna in pastures. Journal of Applied Ecology 13:41–55.

Kirwan, M. L., and J. P. Megonigal. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. Nature 504:53–60.

Van Klink, R., C. Rickert, R. Vermeulen, O. Vorst, M. F. WallisDeVries, and J. P. Bakker. 2013. Grazed vegetation mosaics do not maximize arthropod diversity: evidence from salt marshes. Biological Conservation 164:150–157.

Koch, K. (1989-1995). Die Käfer Mitteleuropas, Ökologie, bd E1-E3.Goecke & Evers, Krefeld.

Kohler, F., F. Gillet, J. M. Gobat, and A. Buttler. 2004. Seasonal vegetation changes in mountain pastures due to simulated effects of cattle grazing. Journal of Vegetation Science 15:143–150.

Koks, B. J., C. Trierweiler, E. G. Visser, C. Dijkstra, and J. Komdeur. 2007. Do voles make agricultural habitat attractive to Montagu's Harrier *Circus pygargus*? Ibis 149:575–586.

Kraft, N. J. B. 2011. Disentangling the drivers of beta diversity along latitudinal and elevational gradients. Science 334:1348.

Krantz, G. W., and D. E. Walter. 2009. A manual of acarology: Third edition. Texas Tech University Press, Lubbock, Texas.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological-control. Science 264:1581–1584.

Kruess, A., and T. Tscharntke. 2002a. Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological Conservation 106:293–302.

Kruess, A., and T. Tscharntke. 2002b. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conservation Biology 16:1570–1580.

L

Laanbroek, H. J. 1990. Bacterial cycling of minerals that affect plant-growth in waterlogged soils - a review. Aquatic Botany 38:109–125.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455–1460.

Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139:1–10.

Larsen, K., F. Purrington, S. Brewer, and D. Taylor. 1996. Influence of sewage sludge and fertilizer on the ground beetle (Coleoptera: Carabidae) fauna of an old-field community. Environmental Entomology 25:452–459.

Lavado, R. S., and M. A. Taboada. 1987. Soil salinization as an effect of grazing in a native grassland soil in the flooding Pampa of Argentina. Soil Use and Management 3:143–148.

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology 28:23–39.

Lawton, J. H., and M. P. Hassell. 1981. Asymmetrical competition in insects. Nature 289:793–795.

Lawton, J. H., and D. Schroder. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature 265:137–140.

Leibold, M. A., and M. A. McPeek. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87:1399–1410.

Lenoir, L., and T. Lennartsson. 2010. Effects of timing of grazing on arthropod communities in semi-natural grasslands. Journal of Insect Science 10.

Lepori, F., and B. Malmqvist. 2009. Deterministic control on community assembly peaks at intermediate levels of disturbance. Oikos 118:471–479.

Lezama, F., S. Baeza, A. Altesor, A. Cesa, E. J. Chaneton, and J. M. Paruelo. 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. Journal of Vegetation Science 25:8–21.

Liddle, M. 1997. Recreation ecology: The ecological impact of outdoor recreation and ecotourism. Chapman & Hall, London.

Lindo, Z., N. N. Winchester, and R. K. Didham. 2008. Nested patterns of community assembly in the colonisation of artificial canopy habitats by oribatid mites. Oikos 117:1856–1864.

Lipiec, J., I. Hakansson, S. Tarkiewicz, and J. Kossowski. 1991. Soil physical-properties and growth of spring barley as related to the degree of compactness of 2 soils. Soil & Tillage Research 19:307–317.

Littlewood, N. A. 2008. Grazing impacts on moth diversity and abundance on a Scottish upland estate. Insect Conservation and Diversity 1:151–160.

Littlewood, N. A., A. J. A. Stewart, and B. A. Woodcock. 2013. Science into practice - how can fundamental science contribute to better management of grasslands for invertebrates? Insect Conservation and Diversity 5:1–8.

Loe, L. E., A. Mysterud, A. Stien, H. Steen, D. M. Evans, and G. Austrheim. 2007. Positive short-term effects of sheep grazing on the alpine avifauna. Biology Letters 3:109–111.

Lorenzen, E. D., D. Nogues-Bravo, L. Orlando, J. Weinstock, J. Binladen, K. A. Marske, A. Ugan, M. K. Borregaard, M. T. P. Gilbert, R. Nielsen, S. Y. W. Ho, T. Goebel, K. E. Graf, D. Byers, J. T. Stenderup, M. Rasmussen, P. F. Campos, J. A. Leonard, K.-P. Koepfli, D. Froese, G. Zazula, T. W. Stafford Jr., K. Aaris-Sorensen, P. Batra, A. M. Haywood, J. S. Singarayer, P. J. Valdes, G. Boeskorov, J. A. Burns, S. P. Davydov, J. Haile, D. L. Jenkins, P. Kosintsev, T. Kuznetsova, X. Lai, L. D. Martin, H. G. McDonald, D. Mol, M. Meldgaard, K. Munch, E. Stephan, M. Sablin, R. S. Sommer, T. Sipko, E. Scott, M. A. Suchard, A. Tikhonov, R. Willerslev, R. K. Wayne, A. Cooper, M. Hofreiter, A. Sher, B. Shapiro, C. Rahbek, and E. Willerslev. 2011. Species-specific responses of Late Quaternary megafauna to climate and humans. Nature 479:359–364.

Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. BioScience 56:311.

Louwe Kooijmans, L. 2012. Holland op z'n wildst? De Vera hypothese getoetst aan de prehistorie. De Levende Natuur 113:62–66.

Luff, M. L. 1966. Abundance and diversity of beetle fauna of grass tussocks. Journal of Animal Ecology 35:189–208.

Lumaret, J. P., N. Kadiri, and M. Bertrand. 1992. Changes in resources: consequences for the dynamics of dung beetle communities. Journal of Applied Ecology 29:349–356.

M

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton.

Madsen, M., B. O. Nielsen, P. Holter, O. C. Pedersen, J. B. Jespersen, K.-M. V. Jensen, P. Nansen, and J. Gronvold. 1990. treating cattle with Ivermectin: effects on the fauna and decompsition of dung pats. Journal of Applied Ecology 27:1–15.

Maes, D., and H. Van Dyck. 2005. Habitat quality and biodiversity indicator performances of a threatened butterfly versus a multispecies group for wet heathlands in Belgium. Biological Conservation 123:177–187.

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

Mandelik, Y., T. Dayan, V. Chikatunov, and V. Kravchenko. 2012. The relative performance of taxonomic vs. environmental indicators for local biodiversity assessment: A comparative study. Ecological Indicators 15:171–180.

Mandema, F. S. 2014. Grazing as a nature management tool - An experimental study of the effects of different livestock species and stocking densities on salt-marsh birds. PhD thesis. University of Groningen.

Mandema, F. S., J. M. Tinbergen, B. J. Ens, and J. P. Bakker. (in press). Spatial diversity in canopy height at Redshank and Oystercatcher nest-sites in relation to livestock grazing. Ardea.

Mandema, F. S., J. M. Tinbergen, B. J. Ens, and J. P. Bakker. 2013. Livestock grazing and trampling of birds' nests: an experiment using artificial nests. Journal of Coastal Conservation 17:409–416.

Marion, B., A. Bonis, and J.-B. Bouzille. 2010. How much does grazing-induced heterogeneity impact plant diversity in wet grasslands? Ecoscience 17:229–239.

Martinsen, G. D., E. M. Driebe, and T. G. Whitham. 1998. Indirect interactions mediated by changing plant chemistry_: Beaver browsing benefits beetles. Ecology 79:192–200.

Mbano, B. N. N., R. C. Malpas, M. K. S. Maige, P. A. K. Symonds, and D. M. Thompson. 1995. The Serengeti regional conservation strategy. Pages 605–616 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II Dynamics, Management, and Conservation of an Ecosystem. University of Chicago Press, Chicago and London.

McCall, B. D., and S. C. Pennings. 2012. Disturbance and recovery of salt marsh arthropod communities following BP Deepwater Horizon oil spill. PloS one 7:e32735.

McCauley, D. J., F. Keesing, T. Young, and K. Dittmar. 2008. Effects of the removal of large herbivores on fleas of small mammals. Journal of Vector Ecology 33:263–268.

McCoy, E. D. 2002. The "'veiled gradients '" problem in ecology. Oikos 99:189–192.

McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92–4.

McNaughton, S. J. 1984. Grazing lawns - Animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

Mcnaughton, S. J. 1986. On plants and herbivores. American Naturalist 128:765–770.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by african grazers. Science 278:1798–1800.

Van der Meijden, R. 2005. Heukels' Flora van Nederland. Wolters-Noordhof, Groningen/Houten, The Netherlands.

Meijer, J. 1973. Die Besiedlung des neuen Lauwerszee polders durch Laufkäfer (Carabidae) und Spinnen (Araneae). Faunistisch-Ökologische Mitteilungen 4:241–254.

Melis, C., I. Teurlings, J. C. Linnell, R. Andersen, and A. Bordoni. 2004. Influence of a deer carcass on Coleopteran diversity in a Scandinavian boreal forest: a preliminary study. European Journal of Wildlife Research 50:146–149.

Meyer, H., H. Fock, A. Haase, H. D. Reinke, and I. Tulowitzki. 1995. Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. Helgolander Meeresuntersuchungen 49:563–589.

Meyer, H., and H.-D. Reinke. 1996. Changes in the biocoenotic structure of the invertebrate fauna of salt-marshes caused by different sheep graving intensities. Faunistisch-Oekologische Mitteilungen 7:109–151.

Mikola, J., H. Setala, P. Virkajarvi, K. Saarijarvi, K. Ilmarinen, W. Voigt, and M. Vestberg. 2009. Defoliation and patchy nutrient return drive grazing effects on plant and soil properties in a dairy cow pasture. Ecological Monographs 79:221–244.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327–366.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132:87–106.

Milsom, T. P., S. D. Langton, W. K. Parkin, S. Peel, J. D. Bishop, J. D. Hart, and N. P. Moore. 2000. Habitat-models of bird species' distribution: an aid to the management of coastal grazing marshes. Journal of Applied Ecology 37:706–727.

Mommertz, S., C. Schauer, N. Kosters, A. Lang, and J. Filser. 1996. A comparison of D-Vac suction, fenced and unfenced pitfall trap sampling of epigeal arthropods in agroecosystems. Annales Zoologici Fennici 33:117–124.

Moon, D. C., and P. Stiling. 2002a. The effects of salinity and nutrients, on a tritrophic salt-marsh system. Ecology 83:2465–2476.

Moon, D., and P. Stiling. 2002b. The influence of species identity and herbivore feeding mode on top-down and bottom-up effects in a salt marsh system. Oecologia 133:243–253.

Moreby, S. J., and C. Stoate. 2000. A quantitative comparison of neck-collar and faecal analysis to determine passerine nestling diet. Bird Study 47:320–331.

Morris, M. G. 1967. Differences between invertebrate faunas of grazed and ungrazed chalk grassland .1. Responses of some phytophagous insects to cessation of grazing. Journal of Applied Ecology 4:459–474.

Morris, M. G. 1971. The management of grassland for the conservation of invertebrate animals. Pages 527 – 552 *in* E. Duffey and A. S. Watt, editors. The scientific management of animal and plant communities for conservation. Blackwell scientific publications, Oxford, London, Edinburgh.

Morris, M. G. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biological Conservation 95:129–142.

Morris, M. G., R. T. Clarke, and W. E. Rispin. 2005. The success of a rotational grazing system in conserving the diversity of chalk grassland Auchenorrhyncha. Journal of Insect Conservation 9:363–374.

Murdoch, W. W., C. H. Peterson, and F. C. Evans. 1972. Diversity and pattern in plants and insects. Ecology 53:819–829.

N

Naeth, M. A., A. W. Bailey, D. J. Pluth, D. S. Chanasyk, and R. T. Hardin. 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of alberta. Journal of Range Management 44:7.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Navarro, L. M., and H. M. Pereira. 2012. Rewilding abandoned landscapes in Europe. Ecosystems 15:900–912.

Negro, M., C. La Rocca, S. Ronzani, A. Rolando, and C. Palestrini. 2013. Management tradeoff between endangered species and biodiversity conservation: The case of *Carabus olympiae* (Coleoptera: Carabidae) and carabid diversity in north-western Italian Alps. Biological Conservation 157:255–265.

Negro, M., A. Rolando, and C. Palestrini. 2011. The impact of overgrazing on dung beetle diversity in the Italian Maritime Alps. Environmental Entomology 40:1081–1092.

New, T. R. 2009. Insect species conservation. Cambridge University Press, New York.

Nickel, H. 2003. The leafhoppers and Planthoppers of Germany (Hemiptera: Auchenorrhyncha). Pensoft publishers, Sophia-Moscow.

Nickel, H., and J. Hildebrandt. 2003. Auchenorrhyncha communities as indicators of disturbance in grasslands (Insecta, Hemiptera) - a case study from the Elbe flood plains (northern Germany). Agriculture Ecosystems & Environment 98:183–199.

Nogues-Bravo, D., M. B. Araujo, T. Romdal, and C. Rahbek. 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453:216–U8.

Nolte, S. 2014. Grazing as a nature management tool - The effect of different livestock species and stocking densities on salt-marsh vegetation and accretion. PhD thesis. University of Groningen.

Nolte, S., P. Esselink, and J. P. Bakker. 2013. Flower production of *Aster tripolium* is affected by behavioral differences in livestock species and stocking densities : the role of activity and selectivity. Ecological Research 82:821-831.

Van Noordwijk, C. G. E., P. Boer, A. A. Mabelis, W. C. E. P. Verberk, and H. Siepel. 2012. Life-history strategies as a tool to identify conservation constraints: A case-study on ants in chalk grasslands. Ecological Indicators 13:303–313.

Van Noordwijk, C. G. E., D. E. Flierman, E. Remke, M. F. WallisDeVries, and M. P. Berg. 2012. Impact of grazing management on hibernating caterpillars of the butterfly *Melitaea cinxia* in calcareous grasslands. Journal of Insect Conservation 16:909–920.

Von Nordheim, H., O. Norden Andersen, J. Thissen, and (eds). 1996. Red lists of biotopes, flora and fauna of the trilateral Wadden Sea area, 1995. Bundesamt für Naturschutz, Bonn-Bad Godesberg.

Norris, K., T. Cook, B. O'Dowd, and C. Durdin. 1997. The density of Redshank *Tringa totanus* breeding on the salt-marshes of the Wash in relation to habitat and its grazing management. Journal of Applied Ecology 34:999.

Novotny, V., Y. Basset, S. E. Miller, G. D. Weiblen, B. Bremer, L. Cizek, and P. Drozd. 2002. Low host specificity of herbivorous insects in a tropical forest. Nature 416:841–844.

Numa, C., J. R. Verdu, C. Rueda, and E. Galante. 2012. Comparing dung beetle species assemblages between protected areas and adjacent pasturelands in a Mediterranean savanna landscape. Rangeland Ecology & Management 65:137–143.

Nykanen, H., and J. Koricheva. 2004. Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. Oikos 104:247–268.

O

Öckinger, E., A. K. Eriksson, and H. G. Smith. 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biological Conservation 133:291–300.

Oertli, S., A. Muller, D. Steiner, A. Breitenstein, and S. Dorn. 2005. Cross-taxon congruence of species diversity and community similarity among three insect taxa in a mosaic landscape. Biological Conservation 126:195–205.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, D. L. Simpson, P. Solymos, M.Henry, H.Stevens, H. Wagner, F. Guillaume Blanchet, P. R. Minchin, R. G. O'Hara, G. L. Simpson, M. Henry, and H. Stevens. 2013. vegan: Community Ecology Package. http://CRAN.R-project.org/package=vegan.

Olff, H., J. De Leeuw, J. P. Bakker, R. J. Platerink, H. J. Van Wijnen, and W. De Munck. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. Journal of Ecology 85:799–814.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13:261–265.

Olff, H., M. E. Ritchie, and H. H. T. Prins. 2002. Global environmental controls of diversity in large herbivores. Nature 415:901–4.

Olff, H., F. W. M. Vera, J. Bokdam, E. S. Bakker, J. M. Gleichman, K. de Maeyer, and R. Smit. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition Plant Biology 1:127–137.

Oliver, I., D. Garden, P. J. Greenslade, B. Haller, D. Rodgers, O. Seeman, and B. Johnston. 2005. Effects of fertiliser and grazing on the arthropod communities of a native grassland in south-eastern Australia. Agriculture Ecosystems & Environment 109:323–334.

Olofsson, J. 2009. Effects of simulated reindeer grazing, trampling, and waste products on nitrogen mineralization and primary production. Arctic Antarctic and Alpine Research 41:330–338.

Olofsson, J., C. de Mazancourt, and M. J. Crawley. 2008. Spatial heterogeneity and plant species richness at different spatial scales under rabbit grazing. Oecologia 156:825–834.

Onsager, J. A. 2000. Suppression of grasshoppers in the Great Plains through grazing management. Journal of Range Management 53:592–602.

Ostermann, O. P. 1998. The need for management of nature conservation sites designated under Natura 2000. Journal of Applied Ecology 35:968–973.

Owensmith, N. 1989. Megafaunal extinctions – the conservation message from 11,000 Years bp. Conservation Biology 3:405–412.

P

Petersen, H., E. Jucevica, and P. Gjelstrup. 2004. Long-term changes in collembolan communities in grazed and non-grazed abandoned arable fields in Denmark. Pedobiologia 48:559–573.

Pétillon, J., A. Georges, A. Canard, J. C. Lefeuvre, J. P. Bakker, and F. Ysnel. 2008. Influence of abiotic factors on spider and ground beetle communities in different salt-marsh systems. Basic and Applied Ecology 9:743–751.

Pétillon, J., A. Georges, A. Canard, and F. Ysnel. 2007. Impact of cutting and sheep grazing on ground-active spiders and carabids in intertidal salt marshes (Western France). Animal Biodiversity and Conservation 30:201–209.

Pétillon, J., F. Ysnel, A. Canard, and J. C. Lefeuvre. 2005. Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: Responses of spider populations. Biological Conservation 126:103–117.

Piearce, T. G. 1984. Earthworm populations in soils disturbed by trampling. Biological Conservation 29: 241–252.

Pimm, S., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132:757–785.

Pinheiro, J., D. Bates, S. DebRoy and D. Sarkar. 2012. nlme: Linear and nonlinear mixed effects models. R package version 3.1-103.

Platnick, N. I. 2013. The world spider catalog, version 14.0. American Museum of Natural History, New York.

Poelman, E. H., N. M. van Dam, J. J. A. van Loon, L. E. M. Vet, and M. Dicke. 2009. Chemical diversity in Brassica oleracea affects biodiversity of insect herbivores. Ecology 90:1863–1877.

Poelman, E. H., J. J. a van Loon, and M. Dicke. 2008. Consequences of variation in plant defense for biodiversity at higher trophic levels. Trends in Plant Science 13:534–41.

Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. Biological Conservation 12:115–134.

Potts, S. G., B. A. Woodcock, S. P. M. Roberts, T. Tscheulin, E. S. Pilgrim, V. K. Brown, and J. R. Tallowin. 2009. Enhancing pollinator biodiversity in intensive grasslands. Journal of Applied Ecology 46:369–379.

Pöyry, J., S. Lindgren, J. Salminen, and M. Kuussaari. 2004. Restoration of Butterfly and Moth Communities in Semi-Natural Grasslands by cattle grazing. Ecological Applications 14:1656–1670.

Pöyry, J., M. Luoto, J. Paukkunen, J. Pykälä, K. Raatikainen, and M. Kuussaari. 2006. Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. Oikos 115:401–412.

Prather, C. M., S. L Pelini, A. Laws, E. Rivest, M. Woltz, C. P. Bloch, I. Del Toro, C.-K. Ho, J. Kominoski, T. A. Scott Newbold, S. Parsons, and A. Joern. 2013. Invertebrates, ecosystem services and climate change. Biological Reviews 88:327–348.

Prendini, L., L.-J. Theron, K. Van der Merwe, and N. Owensmith. 1996. Abundance and guild structure of grasshoppers (Orthoptera: Acridoidea) in communally grazed and protected savanna. South African Journal of Zoology 31.

Prins, H. H. T. 1998. Origins and development of grassland communities in northwestern Europe. Pages 55–107 *in* M. F. Wallis De Vries, J. P. Bakker, and S. E. van Wieren, editors. Grazing and conservation management. Kluwer, Dodrecht.

Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient rich ecosystems. Ecology 79:2581–2592.

Pullin, A. S., and G. B. Stewart. 2006. Guidelines for systematic review in conservation and environmental management. Conservation Biology 20:1647–1656.

Q

Qian, H., S. Chen, L. Mao, and Z. Ouyang. 2013. Drivers of -diversity along latitudinal gradients revisited. Global Ecology and Biogeography 22:659–670.

Qian, H., and R. E. Ricklefs. 2007. A latitudinal gradient in large-scale beta diversity for vascular plants in North America. Ecology letters 10:737–44.

R

R Core Team 2013. R: A language and environment for statistical computing. version 3.0.2. R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.

Ralph, C. P., S. E. Nagata, and J. C. Ralph. 1985. Analysis of droppings to describe diets of small birds. Journal of Field Ornithology 56:165–174.

Raupp, M. J., and R. F. Denno. 1979. Influence of patch size on a guild of sap-feeding insects that inhabit the salt-marsh grass *Spartina patens*. Environmental Entomology 8:412–417.

Redpath, S. M. 1992. Behavioural interactions between Hen Harriers and their moorland prey. Ornis Scandinavica 23:73.

Regge, H. 1973. Die Blattlaus-Arten (Hexapoda, Aphidoidea) des Gezeitenbereichs der Nordseeküste Schleswig-Holsteins. Faunistisch-Ökologische Mitteilungen 4:241–254.

Reid, A. M., and D. F. Hochuli. 2007. Grassland invertebrate assemblages in managed landscapes: Effect of host plant and microhabitat architecture. Austral Ecology 32:708–718.

Reitz, S. R., and J. T. Trumble. 2002. Competitive displacement among insects and arachnids. Annual review of entomology 47:435–65.

Rickert, C. 2011. Microplepidoptera in salt marshes. Faunistisch-Ökologische Mitteilungen Supplement.

Rickert, C., A. Fichtner, R. van Klink, and J. P. Bakker. 2012. Alpha- and beta-diversity in moth communities in salt marshes is driven by grazing management. Biological Conservation 146:24–31.

Rickert, C., R. van Klink, and A. fichtner. (in prep). Grazing decreases predictability in moth community assembly by disrupting plant-herbivore interactions.

Riipi, M., K. Lempa, E. Haukioja, V. Ossipov, and K. Pihlaja. 2005. Effects of simulated winter browsing on mountain birch foliar chemistry and on the performance of insect herbivores. Oikos 111:221–234.

Ripple, W. J., and R. L. Beschta. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biological Conservation 133:397–408.

Ripple, W. J., J. a. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, a. D. Wallach, and a. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influence on insect herbivores in a temperate grassland. Ecology 81:1601–1612.

Roberts, M. J. 1987. The Spiders of Great Britain and Ireland. Harley books, Colchester.

Roberts, M. J. 1995. Spiders of Britain and Northern Europe. HarperCollins Publishers, London.

Rosa-García, R., B. M. Jáuregui, U. García, K. Osoro, R. Celaya. 2009a. Effects of livestock breed and grazing pressure on ground-dwelling arthropods in Cantabrian heathlands. Ecological Entomology 34:466–475.

Rosa-García, R., B. M. Jáuregui, U. García, K. Osoro, R. Celaya. 2009b. Responses of arthropod fauna assemblages to goat grazing management in northern Spanish heathlands. Environmental Entomology 38:985–995.

Rossi, J.-P. 2011. Extrapolation and biodiversity indicators: handle with caution! Ecological Indicators 11:1490–1491.

Rothenwöhrer, C., C. Scherber, and T. Tscharntke. 2013. Grassland management for stem-boring insects: Abandoning small patches is better than reducing overall intensity. Agriculture, Ecosystems & Environment 167:38–42.

Rowe, R. J. 2009. Environmental and geometric drivers of small mammal diversity along elevational gradients in Utah. Ecography 32:411–422.

Roy, D. B., and J. A. Thomas. 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. Oecologia 134:439–444.

Rule, S., B. W. Brook, S. G. Haberle, C. S. M. Turney, A. P. Kershaw, and C. N. Johnson. 2012. The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. Science 335:1483–1486.

Rzanny, M., and W. Voigt. 2012. Complexity of multitrophic interactions in a grassland ecosystem depends on plant species diversity. Journal of Animal Ecology 81:614–627.

S

Saccheri, I., M. Kuussaari, and M. Kankare. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:441–442.

Samways, M. J. 1994. Insect Conservation Biology. Chapman and Hall, London.

Samways, M. J. 2005. Insect diversity conservation. Cambridge University Press, Cambridge.

Samways, M. J., and K. Kreuzinger. 2001. Vegetation, ungulate and grasshopper interactions inside vs. outside an African savanna game park. Biodiversity and Conservation 10:1963–1981.

Sanders, D., and C. Platner. 2007. Intraguild interactions between spiders and ants and top-down control in a grassland food web. Oecologia 150:611–624.

Sanderson, E. W., K. H. Redford, B. Weber, K. Aune, D. Baldes, J. Berger, D. Carter, C. Curtin, J. Derr, S. Dobrott, E. Fearn, C. Fleener, S. Forrest, C. Gerlach, C. C. Gates, J. E. Gross, P. Gogan, S. Grassel, J. A. Hilty, M. Jensen, K. Kunkel, D. Lammers, R. List, K. Minkowski, T. Olson, C. Pague, P. B. Robertson, and B. Stephenson. 2008. The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. Conservation biology 22:252–66.

Schaefer, M. 1974. Experimentele Untersuchungen zur Bedeutung der interspezifischen Konkurrenz bei 3 Wolfspinnen-Arten (Araneida: Lycosidae) einer salzwiese. Zool. Jb. Syst. 101:213–235.

Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E.-D. Schulze, C. Roscher, A. Weigelt, E. Allan, H. Bessler, M. Bonkowski, N. Buchmann, F. Buscot, L. W. Clement, A. Ebeling, C. Engels, S. Halle, I. Kertscher, A.-M. Klein, R. Koller, S. König, E. Kowalski, V. Kummer, A. Kuu, M. Lange, D. Lauterbach, C. Middelhoff, V. D. Migunova, A. Milcu, R. Müller, S. Partsch, J. S. Petermann, C. Renker, T. Rottstock, A. Sabais, S. Scheu, J. Schumacher, V. M. Temperton, and T. Tscharntke. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553–556.

Schile, L., and S. Mopper. 2006. The deleterious effects of salinity stress on leafminers and their freshwater host. Ecological Entomology 31:345–351.

Schmitz, O. J. 2011. Resolving ecosystem complexity. Monographs in Population Biology 47) . Princeton University Press, Princeton.

Scholl, P. J. 1993. Biology and control of cattle grubs. Annual Review of Entomology 38:53–70.

Schon, N. L., A. D. Mackay, and M. A. Minor. 2012. Vulnerability of soil invertebrate communities to the influences of livestock in three grasslands. Applied Soil Ecology 53:98–107.

Schon, N. L., A. D. Mackay, G. W. Yeates, and M. A. Minor. 2010. Separating the effects of defoliation and dairy cow treading pressure on the abundance and diversity of soil invertebrates in pastures. Applied Soil Ecology 46:209–221.

Schrader, S., and M. Lingnau. 1997. Influence of soil tillage and soil compaction on microarthropods in agricultural land. Pedobiologia 41:202–209.

Schrama, M. 2012. The assembly of a salt marsh community – The interplay of green and brown foodwebs. PhD thesis. University of Groningen.

Schrama, M., M. P. Berg, and H. Olff. 2012. Ecosystem assembly rules: the interplay of green and brown webs during salt marsh succession. Ecology 93:2353–2364.

Schrama, M., P. Heijning, J. P. Bakker, M. P. Berg, and H. Olff. 2013a. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. Oecologia 172: 231–243.

Schrama, M., G. F. Veen, E. S. Bakker, J. L. Ruifrok, J. P. Bakker, and H. Olff. 2013b. An integrated perspective to explain nitrogen mineralization in grazed ecosystems. Perspectives in Plant Ecology Evolution and Systematics 15:32–44.

Schröder, H. K., K. Kiehl, and M. Stock. 2002. Directional and non-directional vegetation changes in a temperate salt marsh in relation to biotic and abiotic factors. Applied Vegetation Science 5:33–44.

Scohier, A., A. Ouin, A. Farruggia, and B. Dumont. 2013. Is there a benefit of excluding sheep from pastures at flowering peak on flower-visiting insect diversity? Journal of Insect Conservation 17:287–294.

Seastedt, T. R. 1984. The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29:25–46.

Seastedt, T. R., and D. A. Crossley. 1984. The influence of arthropods on ecosystems. Bioscience 34:157–161.

Seastedt, T. R., R. A. Ramundo, and D. C. Hayes. 1988. Maximization of densities of soil animals by foliage herbivory - empirical-evidence, graphical and conceptual models. Oikos 51:243–248.

Settele, J., O. Kudrna, A. Harpke, I. Kühn, C. Van Swaay, and R. Verovnik. 2008. Climatic Risk Atlas of European Butterflies. Pensoft publishers, Sofia, Moscow.

Shaffer, M. L. 1981. Minimum Population Sizes for Species Conservation. BioScience 31:131–134.

Shaw, M. R. 2006. Habitat Considerations for Parasitic Wasps (Hymenoptera). Journal of Insect Conservation 10:117–127.

Shaw, M. R., and M. E. Hochberg. 2001. The neglect of parasitic Hymenoptera in insect conservation strategies: The British fauna as a prime example. Journal of Insect Conservation 5:253 – 263.

Siegfried, W. R. 1990. Tail length and biting insects of ungulates. Journal of Mammalogy 71:75.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057–2070.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. American Naturalist 152:738–750.

Sirami, C., L. Brotons, I. Burfield, J. Fonderflick, and J.-L. Martin. 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biological Conservation 141:450–459.

Sjödin, N. E., J. Bengtsson, and B. Ekbom. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. Journal of Applied Ecology 45:763–772.

Smit, J. T. 2010. De prachtvlieg *Melieria picta* in grote aantallen op strandkweek *Elytrigia atherica* op Schiermonnikoog (Diptera: Ulidiidae). Nederlandse Faunistische Mededelingen 33:1–8.

Smith, C. C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. Ecology 21:381–397.

Sørensen, L. I., J. Mikola, M.-M. Kytoviita, and J. Olofsson. 2009. Trampling and spatial heterogeneity explain decomposer abundances in a sub-arctic grassland subjected to simulated reindeer grazing. Ecosystems 12:830–842.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of animal ecology 46:336–365.

Srivastava, D. S., and R. L. Jefferies. 1996. A positive feedback: herbivory, plant growth, salinity, and the desertification of an arctic salt-marsh. Journal of Ecology 84:31.

Stewart, K. E. J., N. A. D. Bourn, and J. A. Thomas. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. Journal of Applied Ecology 38:1148–1154.

Stiling, P. D., and D. R. Strong. 1983. Weak competition among *Spartina* stem borers, by means of murder. Ecology 64:770.

Stock, M., S. Gettner, M. Hagge, K. Heinzel, J. Kohlus, and H. Stumpe. 2005. Salzwiesen an der Westküste von Schleswig–Holstein 1988–2001. Schriftenreihe des Nationalparks Schleswig–Holsteinisches Wattenmeer. Boyens Buchverlag, Heide.

Stock, M., and K. Kiehl. 2000. Die Salzwiesen der Hamburger Hallig. Schriftenreihe des Nationalparks Schleswig–Holsteinisches Wattenmeer. Heide.

Stock, M., K. Kiehl, and H.-D. Reinke. 1997. Salzwiesenschutz im schleswig-holsteinischen Wattenmeer. Heide.

Van Straalen, N. M., and P. C. Rijninks. 1982. The efficiency of tullgren apparatus with respect to interpreting seasonal-changes in age structure of soil arthropod populations. Pedobiologia 24:197–209.

Van Straalen, N. M., and H. A. Verhoef. 1997. The development of a bioindicator system for soil acidity based on arthropod pH preferences. Journal of Applied Ecology 34:217–232.

Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants. Community patterns and mechanisms. Blackwell Scientific publications, Oxford.

Suárez-Seoane, S., P. E. Osborne, and J. Baudry. 2002. Responses of birds of different biogeographic origins and habitat requirements to agricultural land abandonment in northern Spain. Biological Conservation 105:333–344.

Suominen, O., and K. Danell. 2006. Effects of large herbivores on other fauna. Pages 383–412 *in* K. Danell, R. Bergstrom, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambrige university press, Cambridge.

Svenning, J. C. 2002. A review of natural vegetation openness in north-western Europe. Biological Conservation 104:133–148.

Van Swaay, C., A. Cuttelod, S. Collins, D. Maes, M. López Munguira, M. Šašić, J. Settele, R. Verovnik, T. Verstrael, M. Warren, M. Wiemers, and I. Wynhof. 2010. European Red List of Butterfies. Luxembourg.

T

Tallamy, D. W., and R. F. Denno. 1979. Responses of sap-feeding insects (Homoptera-Hemiptera) to simplification of host plant structure. Environmental Entomology 8:1021–1028.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284.

Terborgh, J. 1988. The big things that run the world-a sequel to E. O. Wilson. Conservation Biology 2:402–403.

Terborgh, J., and K. Feeley. 2010. Propagation of trophic cascades via multiple pathways in tropical forests. Pages 125–140 *in* J. Terborgh and J. A. Estes, editors. Trophic cascades - Predators, prey, and the changing dynamics of nature. Island Press, Washington, DC.

Tews, J., U. Brose, V. Grimm, K. Tielborger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

Thomas, C. F. G., P. Brain, and P. C. Jepson. 2003. Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. Journal of Applied Ecology 40:912–927.

Thomas, J. A. 1983. The Ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lycaenidae) in Britain. Journal of Applied Ecology 20:59–83.

Thomas, J. A. 1993. Holocene climate changes and warm man-made refugia may explain why a 6th of British butterflies possess unnatural early-successional habitats. Ecography 16:278–284.

Thomas, J. A., M. G. Morris, and C. Hambler. 1994. Patterns, mechanisms and rates of extinction among invertebrates in the United-Kingdom. Philosophical Transactions of the Royal Society of London 344:47–54.

Thomas, J. A., D. J. Simcox, and R. T. Clarke. 2009. Successful conservation of a threatened *Maculinea* butterfly. Science 325:80–3.

Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T. Clarke, and J. H. Lawton. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303:1879–1881.

Thomas, J. A., C. D. Thomas, D. J. Simcox, and R. T. Clarke. 1986. Ecology and declining status of the Silver-Spotted Skipper butterfly (*Hesperia comma*) in Britain. Journal of Applied Ecology 23:365–380.

Thompson, R., and C. Townsend. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. Journal of Animal Ecology 75.

Tilman, D. 1986. A Consumer-resource approach to community structure. American Zoologist 26:5–22.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Tischler, T., A. Mieth, H. Meyer, H. D. Reinke, I. Tutlowitzki, H. Fock, and A. Haasse. 1994. Ökosystemsforschung Wattenmeer Schleswig-Holstein – Teilvorhaben A 5.3 Bioindikatoren im Supralitoral, Teilbericht B: Ökologie von Salzwiesenarten und Salzwiesen-Lebensgemeinschaften – Wirbellosenfauna. . Kiel.

Traill, L. W., C. J. A. Bradshaw, and B. W. Brook. 2007. Minimum viable population size: A meta-analysis of 30 years of published estimates. Biological Conservation 139:159–166.

Traill, L. W., B. W. Brook, R. R. Frankham, and C. J. A. Bradshaw. 2010. Pragmatic population viability targets in a rapidly changing world. Biological Conservation 143:28–34.

Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London Series B-Biological Sciences 270:467–473.

Treherne, J. E., and W. A. Foster. 1977. Diel activity of an intertidal beetle, *Dicheirotrichus gustavi* Crotch. Journal of Animal Ecology 46:127–138.

Trimble, S. W., and A. C. Mendel. 1995. The cow as a geomorphic agent - a critical-review. Geomorphology 13:233–253.

Tscharntke, T. 1997. Vertebrate effects on plant-invertebrate food webs. Pages 277–297 *in* K. Gange and V. K. Brown, editors. Multitrophic interactions in terrestrial ecosystems. Blackwell Science, Oxford.

Tscharntke, T., and H. J. Greiler. 1995. Insect communities, grasses, and grasslands. Annual Review of Entomology 40:535–558.

Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fruend, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87:661–685.

Turin, H. 2000. De Nederlandse Loopkevers; verspreiding en ecologie (Coleoptera: Carabidae). Nederlandse Fauna. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS Nederland, Leiden.

U

Undersander, D., B. Albert, D. Cosgrove, D. Johnson, Pe, and P. Terson. 2002. Pastures for profit: A guide to rotational grazing. University of Wisconsin Extension, Madison.

V

Vanbergen, A. J., R. S. Hails, A. D. Watt, and T. H. Jones. 2006. Consequences for host-parasitoid interactions of grazing-dependent habitat heterogeneity. Journal of Animal Ecology 75:789–801.

Vandenberghe, C., G. Prior, N. A. Littlewood, R. Brooker, and R. Pakeman. 2009. Influence of livestock grazing on meadow pipit foraging behaviour in upland grassland. Basic and Applied Ecology 10:662–670.

Vanhinsbergh, D. P., and D. E. Chamberlain. 2001. Habitat associations of breeding Meadow Pipits *Anthus pratensis* in the British uplands. Bird Study 48:159–172.

Veeneklaas, R., A. Bockelmann, T. Reusch, and J. Bakker. 2011. Effect of grazing and mowing on the clonal structure of *Elytrigia atherica*: a long-term study of abandoned and managed sites. Preslia 83:455–470.

Veeneklaas, R. M. 2013. Adaptation and dispersal of the native invasive salt marsh species *Elytrigia atherica*. PhD thesis. University of Groningen.

Vera, F. W. M., E. S. Bakker, and H. Olff. 2006. Large herbivores: missing partners of western European light-demanding tree and shrub species? Pages 203–231 *in* K. Danell, P. Duncan, R. Bergström, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge.

Verberk, W. C. E. P., C. G. E. van Noordwijk, and A. G. Hildrew. 2013. Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. Freshwater Science 32:531–547.

Verdu, J. R., C. E. Moreno, G. Sanchez-Rojas, C. Numa, E. Galante, and G. Halffter. 2007. Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. Biological Conservation 140:308–317.

Verhoeven, J. T. A. 1980. Human influences on the landscape of the Wadden Sea area. *in* K. S. Dijkema, H.-E. Reineck, and W. J. Wolff, editors. Geomorphology of the Wadden Sea Area. Report 1 of the Wadden Sea Working Group. Balkema, Rotterdam.

Verschoor, B. C., and B. P. M. Krebs. 1995a. Diversity changes in a plant and carabid community during early succession in an embanked salt-marsh area. Pedobiologia 39:405–416.

Verschoor, B. C., and B. P. M. Krebs. 1995b. Successional changes in a salt-marsh carabid beetle (Coleoptera, Carabidae) community after embankment of the Markiezaat area. Pedobiologia 39:385–404.

Versteegde, L. B. 2011. Changing patterns - the influence of stress on vegetation patterns in a salt marsh. Msc thesis. University of Groningen.

Vessby, K., B. Söderström, A. Glimskar, and B. Svensson. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. Conservation Biology 16:430–439.

Vicari, M., and D. R. Bazely. 1993. Do grasses fight back? The case for antiherbivore defences. Trends in ecology & evolution 8:137–41.

Vickery, J. A., J. R. Tallowin, R. E. Feber, E. J. Asteraki, P. W. Atkinson, R. J. Fuller, and V. K. Brown. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38:647–664.

De Vlas, J., F. S. Mandema, S. Nolte, R. van Klink, and P. Esselink. 2013. Nature conservation of salt marshes - The influence of grazing on biodiversity. It Fryske Gea, Olderterp.

Völkl, W., H. Zwölfer, M. Romstöck-Völkl, and C. Schmelzer. 1993. Habitat management in calcareous grasslands: effects on the insect community developing in flower heads of *Cynarea*. Journal of Applied Ecology 30:307–315.

Vorst, O. 2010. Catalogus van de Nederlandse kevers (Coleoptera). (O. Vorst, Ed.). Monografiën van de Nederlandse Entomologische Vereniging 11. Nederlandse Entomologische Vereniging, Amsterdam.

Vreysen, M. J. B., K. M. Saleh, M. Y. Ali, A. M. Abdulla, Z. R. Zhu, K. G. Juma, V. A. Dyck, A. R. Msangi, P. A. Mkonyi, and H. U. Feldmann. 2000. *Glossina austeni* (Diptera : Glossinidae) eradicated on the Island of Unguja, Zanzibar, using the sterile insect technique. Journal of Economic Entomology 93:123–135.

Vulliamy, B., S. G. Potts, and P. G. Willmer. 2006. The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos 114:529–543.

W

Wachmann, E., E. Melber, and J. Deckert. (2003–2008). Wanzen. Band 1-4. Goecke & Evers, Keltern.

Wall, R., and L. Strong. 1987. Environmental consequences of treating cattle with the antiparasitic drug Ivermectin. Nature 327:418–421.

WallisDeVries, M. F. 1998. Large herbivores as key factors for nature conservation. Pages 1–20 *in* M. F. WallisDeVries, J. P. Bakker, and S. E. Van Wieren, editors. Grazing and conservation management. Kluwer, Dordrecht.

WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. Oecologia 121:355–363.

WallisDeVries, M. F., A. E. Parkinson, J. P. Dulphy, M. Saye, and E. Diana. 2007. Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity. Grass and Forage Science 62:185–197.

Wallisdevries, M. F., C. A. M. Van Swaay, and C. L. Plate. 2012. Changes in nectar supply: A possible cause of widespread butterfly decline. Current zoology 58:384–391.

Walton, K. C. 1979. Diet of Meadow Pipits *Anthus pratensis* on Mountain Grassland in Snowdonia. Ibis 121: 325–329.

Wanner, A., S. Suchrow, K. Kiehl, W. Meyer, N. Pohlmann, M. Stock, and K. Jensen. 2014. Scale matters: Impact of management regime on plant species richness and vegetation type diversity in Wadden Sea salt marshes. Agriculture, Ecosystems & Environment 182:69–79.

Ward, D. F., T. R. New, and A. L. Yen. 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. Journal of Insect Conservation 5:47–53.

Wardle, D. A., G. M. Barker, G. W. Yeates, K. I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences. Ecological Monographs 71:587–614.

Weeda, E. J. 1999. De Nederlandse Oecologische Flora. . KNNV Uitgeverij, Amsterdam.

Weigmann, G. 2006. Hornmilben (Oribatida) : Acari, Actinochaetida. Page 520 Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach den Merkmalen und nach ihrer Lebensweise. Goecke & Evers, Keltern.

White, T. C. R. 1993. The Inadequate Environment. Nitrogen and the Abundance of Animals. Springer-Verlag, Berlin.

Whitehouse, M. E. A., E. Shochat, M. Shachak, and Y. Lubin. 2002. The influence of scale and patchiness on spider diversity in a semi-arid environment. Ecography 25:395–404.

Whitman, W. B., D. C. Coleman, and W. J. Wiebe. 1998. Prokaryotes : The unseen majority. Proceedings of the National Academy of Sciences 95:6578–6583.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:280–338.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143:2280–2291.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: Pattern, Process, Scale, and Synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Wilson, E. O. 1987. The little things that run the world (the importance and conservation of invertebrates). Conservation Biology 1:344–346.

Wilson, G. W. C. 1986. Control of Warble Fly in Great-Britain and the European-Community. Veterinary Record 118:653–656.

Wilson, J. B., R. K. Peet, J. Dengler, and M. Pärtel. 2012. Plant species richness: the world records. Journal of Vegetation Science 23:796–802.

Wilson, J. D., B. E. Arroyo, and S. C. Clark. 1996. The diet of bird species of lowland farmlan, a literature review. Department of the environment and English nature, Oxford.

Wise, D. H., D. M. Moldenhauer, and J. Halaj. 2006. Using stable isotopes to reveal shifts in prey consumption by generalist predators. Ecological Applications 16:865–876.

Woodcock, B. A., J. M. Bullock, S. R. Mortimer, and R. F. Pywell. 2012. Limiting factors in the restoration of UK grassland beetle assemblages. Biological Conservation 146:136–143.

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

Woodcock, B. A., and R. F. Pywell. 2009. Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. Biodiversity and Conservation 19:81–95.

Woodcock, B. A., I. N. Vogiatzakis, D. B. Westbury, C. S. Lawson, A. R. Edwards, A. J. Brook, S. J. Harris, K. A. Lock, N. Maczey, G. Masters, V. K. Brown, and S. R. Mortimer. 2010. The role of management and landscape context in the restoration of grassland phytophagous beetles. Journal of Applied Ecology 47:366–376.

Wright, J., C. Both, P. A. Cotton, and D. Bryant. 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. Journal of Animal Ecology 67:620–634.

X

Xie, Z., P. H. Williams, and Y. Tang. 2008. The effect of grazing on bumblebees in the high rangelands of the Eastern Tibetan Plateau of Sichuan. Journal of Insect Conservation 12:695–703.

Y

Ydenberg, R. C., and H. H. T. Prins. 1981. Spring grazing and the manipulation of food quality by Barnacle Geese. Journal of Applied Ecology 18:443–453.

Yoshihara, Y., B. Chimeddorj, B. Buuueibaatar, B. Lhaquasuren, and S. Takatsuki. 2008. Effects of livestock grazing on pollination on a steppe in eastern Mongolia. Biological Conservation 141:2376–2386.

Z

Zaslavski, V. 1988. Insect development: Photoperiodic and temperature control. Springer-Verlag, Berlin.

Zeder, M. A. 2008. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. Proceedings of the National Academy of Sciences 105:11597–11604.

Zhu, H., D. Wang, L. Wang, Y. Bai, J. Fang, and J. Liu. 2012. The effects of large herbivore grazing on meadow steppe plant and insect diversity. Journal of Applied Ecology 49:1075–1083.

Summary
Samenvatting

SUMMARY

Of dwarves and giants – how large herbivores shape arthropod communities on salt marshes

Grazing by large herbivores is an increasingly applied management practice in nature conservation with the aim of maintaining open, botanically rich landscapes. The effects of grazing on arthropods are rarely considered, however, despite the fact that arthropods form the most species-rich group of eukaryotic organisms on earth.

Also on coastal salt marshes grazing is often applied to prevent the dominance of the coarse grass *Elytrigia atherica*. Salt marshes are regularly inundated by sea water, and the plants and invertebrates living here are well adapted to these extreme conditions. Several species are restricted to the salt marshes of Western Europe, and for this reason, the Netherlands have a great responsibility for the protection of these species.

The salt marshes of the Netherlands have been used by humans for some 2600 years, mostly in the form of livestock grazing. Since in the second half of the 20t^{h} century livestock grazing became economically less feasible, many salt marshes fell to abandonment. By contrast, on the Northern German salt marshes, livestock grazing was ceased for reasons of nature conservation, and a general laissez-fair policy. Over time, it became clear that abandonment of salt marshes would lead to an encroachment and later total dominance of E. *atherica* and a decrease in especially short-statured plant species and their associated herbivorous insects. Grazing at low stocking densities has successfully been applied to prevent this dominance and restore plant species richness. It has remained unclear, however, how grazing can best be applied to also provide suitable conditions for invertebrates and breeding birds, two groups which have received little attention in grazing research until recently.

To test the effects of different types of grazing management, a large-scale grazing experiment has been installed at the Friesian mainland coast in the area Noord-Friesland Buitendijks. Five different grazing treatments were compared: horse and cattle grazing, each in two densities: one animal per hectare and half an animal per hectare, and additionally rotational grazing with yearly rotations of one head of cattle per hectare and no grazing. The effects of these treatements were studied on plants (see Nolte 2014), birds (Mandema 2014) and invertebrates (this thesis).

Effects of large herbivores on arthropod diversity (chapter 2)

The effect of grazing on arthropod communities has received only a fraction of the attention directed towards the effects on plant communities. This is not only evident for salt marshes, but for all grazed ecosystems around the world. For this reason a systematic review of scientific literature published until 2013 was performed. In total 140 studies were found, of which 24 could be used to quantitatively compare the difference in effects between plants and arthropods.

We found that arthropod species richness was on average decreased by grazing, while plant species richness was as often positively as negatively affected. Additionally, there was a weak positive relation between response of plant and arthropod species richness.

To explain these results, we explored the mechanisms by which large herbivores affect arthropod communities. Five mechanisms were of importance: Direct effects, such as the availability of dung, cadavers and living tissue will have positive effects on arthropods depending on these resources, but trampling and ingestion will have negative effects. Secondly, vegetation structural complexity is strongly affected by herbivores. In short vegetation with bare soil, temperatures can be high, which is beneficial for many species. On the other hand, tall vegetation can provide refuge from climatic extremes, predators and creates possibilities for vertical niche differentiation and has additional resources such as stems and flowers. Logically, one would therefore expect that a mosaic of short and tall vegetation would harbour highest species richness of arthropods, but evidence is scarce (see also chapter 4). Third, large herbivores affect plant species richness, where usually more plant species occur under grazing. This, however, does not imply that the arthropod species specialised on these plant species can actualy utilise these plants, for example because required plant structures are not present, or because of an unfavourable microclimate (see also box I and II). A fourth mechanism works through the soil. Large herbivores apply pressure to the soil, causing the soil to get compacted and decreasing in air-filled porosity. It was unclear whether this would also affect above-ground fauna (see also chapter 5). A fifth and also poorly understood mechanism is the cascading effects in the arthropod foodweb itself. It has been postulated that large herbivores cause a shortening of foodchain lengths by decreasing abundances of the less abundant species high in the trophic chain, but experimental evidence is scare here.

This mechanistic framework shows that nature management using large herbivores can only have positive effects on arthropod diversity if these herbivores create enough heterogogeneity in resources to offset any negative effects.

Effects of grazing on salt-marsh arthropods along a salt-marsh inundation gradient (chapter 3)

In order to gain more insight into the specific conditions on salt marshes, I compared the effects of grazing on arthropod communities (spiders, ground beetles and shore bugs) along the inundation gradient of two salt marshes along the Dutch Wadden Sea: the foreland marsh of Noord-Friesland Buitendijks and the island marsh of Schiermonnikoog. It was expected that with an increase in adverse conditions (flooding frequency) a decrease in species richness and a decrease in variability of the community (β-diversity) would be found.

General support was found for this expectation, but the effects differed between species specialised on salt marshes and non-specialist species. Non-specialised species decreased in species richness with increasing inundation frequency, and their β-diversity was highest on the ungrazed high marsh and the grazed low marsh. Species specialised on salt marshes showed the opposite pattern, and showed highest β-diversity on the ungrazed low marsh, while their species richness was unaffected. Beta-diversity thus peaked under benign and under adverse conditions. However, what should be seen as benign or adverse depended on the habitat specialisation to the salt-marsh specific conditions of the species.

Long-term effects of grazing and cessation on salt marsh arthropods (chapter 4)

On three salt marshes in northern Germany experimental grazing with three sheep stocking densities (ungrazed, moderate density (4 sheep ha^{-1}) and high density (10 sheep ha^{-1}) has taken place for over 20 years. This presented an opportunity to study the long-term effects of these different stocking densities on arthropod communities.

Under moderate stocking densities, the sheep created stable mosaics of short and tall vegetation, by grazing selectively for nutrient-rich regrown vegetation. In contrast to the previously mentioned hypothesis that this should lead to higher arthropod species richness than in homogeneous vegetation, it was found that these grazed mosaics were equally rich in species as homogeneous tall ungrazed vegetation. The mosaics did harbour more species than the homogeneous short grazed vegetation under high stocking densities. Most of the arthropod species showed a clear preference for either tall or short vegetation, and only few reached highest densities in the vegetation mosaics. For the salt marsh specific arthropods this was caused by the high denities of their host plants *Artemisia maritima* and *Juncus gerardii*, which are generally avoided by sheep.

Disentangling the effects of soil compaction and defoliation on plants and soil fauna (chapter 5)

In order to disentangle the mechanisms by which large herbivores affect ecosystems, a full facorial experiment of defoliation by mowing and soil compaction using a rammer was installed on an ungrazed salt marsh at Noord-Friesland Buitendijks. These treatments were compared to the long-term grazed marsh (1 head of cattle ha^{-1}) in the grazing experiment.

We found large differences between the treatments on plants, epigeic fauna (spiders and beetles) and soil microarthropods (springtails and mites). While the epigeic fauna responded primarily to defoliation, the soil microarthropods responded to soil compaction only. The plant community was affected by both treatments, although the effect of defoliation was much stronger than that of soil compaction. None of the groups resembled the community of the grazed marsh, although plants showed a trend in that direction. We conclude that soil compaction by large grazers has an, until now, underappreciated effect on the salt-marsh ecosystem.

Flower-visiting insects under different grazing treatments (chapter 6)

In the grazing experiment at the Friesian coast I investigated the effects of different grazing treatmenst on flower visiting insects. This was done by counting both flower-visiting insects (butterflies, bees and hover flies) and their floral resources along transects through each of the experimental fields.

Horse grazing at high densities proved highly detrimental to both the abundance of flowers and the abundance of flower-visiting insects. More positive effects were found for grazing at low densities with either cattle or horses and during the ungrazed year of the rotational grazing treatment.

The determining factor for abundance of flower visiting insects was the abundance of high-quality floral resources, in particular tall Asteraceae such as *Aster tripolium*, *Cirsium arvense*, and *Tripleurospermum maritimum*. Abundance of the flowers of these species in combination with year effects explained 89% of the variation recorded, and therefore seems to be a reliable indicator for habitat quality of salt marshes for flower-visiting insects.

Diet and foraging behaviour of breeding Meadow Pipits on grazed salt marshes (chapter 7)

Arthropods form the main food source for many breeding bird species, but, as decribed above, are strongly affected by large herbivores. Therefore we were interested in the diet and choice of fouraging locations of Meadow Pipits (*Anthus pratensis*) breeding on grazed salt marshes.

Faecal analysis showed that large spiders (> 5 mm) and caterpillars (ca. 2 cm) formed the main food sources for nestling Meadow Pipits. These groups were proportionally more abundant in the faeces than on the sampled salt marshes, while other in the field very abundant groups, such as small beetles and spiders (< 5 mm) were underrepresented in the faeces.

It was hypothesised that breeding Meadow Pipits would preferentially forage in vegetation characterised by many transitions of tall and short vegetation, as this should maximise the abundance and accessibility of prey, but were unable to find evidence for this hypothesis. Meadow Pipits fouraged in relatively homogeneous vegetation, but we found no difference in mean vegetation height between fouraging locations and control location.

This shows that the presence of a fine-grained vegetation mosaic is not necessarily beneficial to breeding birds, but also shows that additional research is needed to clarify the relationship between the properties of mosaic vegetation and its effects on foraging birds and their prey.

The importance of host plant condition and microclimate for herbivorous insects (Box I & II)

In order to understand how herbivorous insects are affected by modification of their host plant and its microclimate by large herbivores, we studied the effects of grazing on the insects living on *Aster tripolium*. We found that during the ungrazed year, the rotational treatment was highly beneficial to the number of insect individuals and species per individual plant in comparison to both cattle grazing and long term cessation of grazing. This was mostly explaind by plant weight, which correlated well with flower number and size of the plant.

In order to see whether these results also apply to other plant species, I conducted an experiment, manipulating plant biomass (clipping) and microclimate (shading by surrounding vegetation) on five halophytes: *Aster tripolium*, *Artemisia maritima*, *Plantago maritima*, *Puccinellia maritima* and *Festuca rubra*.

For *Aster tripolium* again plant biomass was the best predictor of total insect abundance, which in turn was determined by the clipping treatment. Also for *Artemisia maritima* evidence for the importance of biomass was found, but here shading by surrounding vegetation to a large extent determined plant biomass. Seedings of this species thus depend on high light availability, but mature plants are relatively resistant to encroaching tall grasses (see also chapter 4). The insects living on *Puccinellia maritima* and *Festuca rubra* were hardly affected by plant size, but strongly by microclimate. Insect densities were highest on plants that were not shaded by the surrounding vegetation. On *Plantago maritima* no herbivorous insects were found, despite the fact that these species were present on this salt marsh.

Conclusions for salt-marsh management (chapter 8)

Nature management on salt marshes should be aimed at conservation of all species of plants, vertebrates and invertebrates that depend on this habitat. Because my research indicates that it is unlikely that all these species (see box III for a list of invertebrate species dependent on salt marshes) can be accommodated under one management regime, it can be recommended to maintain both grazed and ungrazed salt marshes in close proximity. How grazing can best take place is an important consideration, and the consequences of different management decision are discussed below.

Cessation of grazing will cause large tracts of salt marsh to be dominated by *E. atherica*. Only places with poor drainage will not be dominated, and these will provide very suitable conditions for many arthropod species. But also in the vegetation dominated by *E. atherica* many salt-marsh specific species will thrive, although most short-statured plant species will disappear, and it is unclear if and how this can be reversed. Grazing will therefore be necessary to conserve these species.

There is not much evidence that the choice of livestock species will have consequenses for arthropods, despite the large differences in diet and behaviour (see Nolte 2014 and Mandema 2014). Because the horses used during this research were heavier and spent approximately 1.7 times as much time grazing than the cattle (Nolte 2014), it is likely that the differences found on the arthropod communities (see chapter 6 and Fig. 8.2) were largely caused by differences in herbivore biomass per hectare. It must be noted, however, that horses cause more trampling than cattle do, and are therefore, also after correction for biomass and intake rate, likely to have somewhat more negative effects on both invertebrates and birds.

By contrast, the choice of stocking density has large consequenses for arthropods. While grazing at high stocking densities has no conservation benefit for salt-marsh arthropods whatsoever, grazing at moderate densities has positive effects, especially on species that live on plants that are avoided by large herbivores. Grazing at low stocking densities will benefit many species, but will probably cause *E. atherica* to spread to a certain extent.

Rotational grazing has emerged as a promising management option, although its long-term effects are not yet known. During ungrazed years, grazing sensitive plant- and arthropod species will be able to increase in population size, which can buffer them against the more adverse conditions during grazed years. The reverse will be evident for species that benefit from grazing. During grazed years it will be important to consider that grazing at high stocking densities is likely to destroy most populations of grazing sensitive species. I recommend a maximum stocking density of 1 head of cattle ha^{-1}, while grazing with 1 horse ha^{-1}, is probably detrimental due to high trampling rates. Elytrigia atherica will show some spread under rotational grazing, but this will be beneficial for many arthropod species.

Monitoring of arthropods

It is important to monitor the effects of nature management on the targeted species. But because moitoring of arthropod populations requires much time and expertise, it is for nature managers important to be able to make use of easily measurable indicators. During my research I found some indicators that can be used to monitor several arthropod species:

- For arthropod species feeding on unpalatable host plants (*Artemisia maritima*, *Juncus maritimus* and under sheep grazing also *J. gerardii*), host plant cover and biomass are a good indicator of abundance and richness of their herbivorous fauna. For many other plant species, and in particular grasses, cover percentage is a poor and sometimes even negative predictor of their potential fauna.
- For flower-visiting insects and the insects specialised on *A. tripolium*, flower abundance is a reliable indicator of insect abundance and species richness per plant. The number of flowers per plant correlates well with its total biomass and the number of herbivorous species living on it. The number of flowers per management unit (estimated in abundance classes) is a reliable indicator for the number of flower-visiting insects that can occur. On salt marshes with other important nectar sources, such as *Limonium vulgare* and *Armeria maritima*, the importance of these species for flower-visiting insects should first be investigated.

Summarised management recommendations for the conservation of salt-marsh arthropods

- **Grazing at high stocking densities** (1 horse / ca. 1.5 head of cattle / 10 sheep ha^{-1}) **has no conservation value for arthopods**.
- **Ungrazed salt marshes**, even those dominated by *E. atherica* or *Atriplex portulacoides* have conservation value for invertebrates such as the endemic moneyspider *Praestigia duffeyi*, which only occurs on ungrazed lower salt marshes.
- There is much evidence that temporary cessation of grazing, as happens during rotational grazing, is beneficial to many invertebrate species. The period of cessation may last for several years, but it must be remembered that as soon as plant species disap-

pear, their associated fauna will disappear as well. When grazing is resumed, the herbivore density will determine which of the arthropod species will be able to persist.

- **Grazing at moderate stocking densities** (0.5 horse / 1 head of cattle / 3-4 sheep ha^{-1}) **will lead to a mosaic of short and tall vegetation**, which can benefit unpalatable plant species and their associated herbivorous fauna.
- **Grazing at low stocking densities** (0.5 cow / 1-3 sheep ha^{-1}) can be beneficial to edible plant species such as *A. tripolium* and its fauna, but will probably also lead to the spread of *E. atherica*.
- **I recommend that these last four management options are maintained at all times in close proximity**, thereby maximising the possibilities for all targeted species. A mosaic of these management regimes with a rotation over several decades, should guarantee the conservation of all species confined to salt marshes.

NEXT STEPS

Many aspects of grazing of salt marshes on plants, birds and especially invertebrates remain to be studied. The first and most important of which is the long term effect of the different regimes, and especially of the promising rotational grazing treatment. Secondly, I have been able to study only a limited number of arthropod species, while the effects on some very species groups such as flies and parasitic wasps remain largely unknown. Thirdly, it will be important to develop easily measurable, but reliable environmental indicators for the majority of salt-marsh species. The list of species and their response to grazing in box III can provide directions. Finally, it will be important to establish what the environmental requirements of rare species are, and how they are affected by management.

SAMENVATTING

Over dwergen en reuzen: hoe grote herbivoren gemeenschappen van ongewervelden beïnvloeden

In natuurbeheer worden steeds vaker grote herbivoren ingezet met als doel om plantensoortenrijke, open landschappen te behouden. Hierin worden de effecten op insecten en andere geleedpotigen dikwijls over het hoofd gezien, ondanks het feit dat dit de meest soortenrijke groep meercellige organismen op aarde is.

Ook op kwelders worden vaak grote herbivoren ingezet om te voorkomen dat de vegetatie gedomineerd raakt door het hoge, taaie gras Zeekweek (*Elytrigia atherica*). Kwelders zijn de buitendijkse graslanden die regelmatig tijdens hoge vloed door zeewater overstromen. De planten en ongewervelden die hier leven zijn doorgaans goed aangepast aan deze extreme omstandigheden en de meeste soorten komen dan ook alleen op kwelders voor. Er zijn zelfs soorten die uitsluitend voorkomen op de kwelders van Noord-West Europa, en Nederland heeft daarom een grote verantwoordelijkheid voor het behoud van deze soorten.

De Nederlandse kwelders worden al zo'n 2600 jaar door mensen gebruikt, vooral in de vorm van beweiding met vee. Nadat in de tweede helft van de vorige eeuw de beweiding van kwelders op veel plaatsen niet meer rendabel bleek, werd hier op veel plaatsen mee gestopt. Op de kwelders van Noord-Duitsland werd dit juist gedaan om redenen van natuurbeheer. Hierdoor werd gaandeweg duidelijk dat het stoppen van beweiding tot gevolg zou hebben dat grote delen van de kwelders overwoekerd zouden raken door Zeekweek, en dat daardoor veel plantensoorten en de daaraan gebonden insecten zou verdwijnen. Beweiding met lage dichtheden met succes ingezet om deze overwoekering tegen te gaan en soortenrijkdom van planten te herstellen. Het is echter nog niet duidelijk hoe beweiding het beste ingezet kan worden, om ook de habitatkwaliteit voor ongewervelden en broedvogels te waarborgen, twee groepen die tot nu toe beperkt aandacht hebben gekregen bij beweidingsonderzoek.

Om deze reden is aan de Friese vastelandskust, in het door de Friese natuurbeschermingsorganisatie It Fryske Gea beheerde terrein Noord-Friesland Buitendijks, een grootschalige beweidingsproef opgezet met vijf behandelingen: paardenbeweiding en runderbeweiding, elk in twee dichtheden: één dier per hectare en een half dier per hectare, en rotatiebeheer met jaarlijkse rotatie van één rund per hectare en geen beweiding. De effecten van deze beweiding zijn onderzocht aan planten (zie Nolte 2014), vogels (zie Mandema 2014) en ongewervelden, waarvan hier verslag is gelegd.

Effecten van grote herbivoren op soortenrijkdom van insecten en spinnen

(hoofdstuk 2)

Er is veel minder onderzoek gedaan naar de effecten van beweiding op geleedpotigen dan de effecten op planten. Dit geldt niet alleen voor kwelders, maar voor beweide ecosystemen wereldwijd. Om deze reden heb ik in samenwerking met andere onderzoekers een overzicht gemaakt van de tot 2013 verschenen literatuur. In totaal hebben we 140 studies gevonden, waarvan er 24 geschikt waren om de effecten van beweiding op soortenrijkdom van ongewervelden te vergelijken met die van soortenrijkdom van planten.

We vonden dat de soortenrijkdom van ongewervelden gemiddeld negatief beïnvloed werd door beweiding, terwijl de soortenrijkdom van planten even vaak positief als negatief beïnvloed werd. Bovendien was er weliswaar een positief, maar zeer zwak verband tussen respons van soortenrijkdom van planten en die van ongewervelden.

Dit gegeven noopte ons tot het uitzoeken van de mogelijke mechanismen die kunnen verkaren waarom de soortenrijkdom van ongewervelden zo vaak negatief wordt beïnvloed door beweiding. Hiertoe hebben we een mechanistisch raamwerk opgesteld (Fig. 9.1) dat beschrijft hoe ongewervelden worden beïnvloed door grote herbivoren. Vijf mechanismen bleken belangrijk: Directe effecten, zoals de beschikbaarheid van mest, kadavers en levend weefsel zullen positieve effecten hebben op de soorten die daarvan afhankelijk zijn, maar anderzijds zullen vertrapping en vraat negatieve effecten hebben. Ten tweede wordt de structuur van de vegetatie sterk beïnvloed door grote herbivoren. In korte vegetatie met veel kale grond zal de temperatuur hoog kunnen oplopen, wat voor veel soorten positief is, anderzijds biedt hoge vegetatie bescherming tegen uitdroging en tegen predatoren, mogelijkheden om vertikaal verschillende niches te bezetten, en zijn er meer belangrijke plantenstructuren aanwezig, evenals bloemen. Het ligt daarom voor de hand dat in een door grote herbivoren gecreëerd mozaïek van hoge en lage vegetatie de soortenrijkdom aan ongewervelden het hoogst zou moeten zijn, maar helaas is hiervoor niet veel bewijs. In hoofdstuk 4 heb ik deze hypothese zelf ook op kwelders getest, maar er geen bewijs voor gevonden. Ten derde beïnvloeden grote herbivoren de soortenrijkdom van planten, waarbij doorgaans meer plantensoorten aanwezig zijn onder beweiding. Dit betekent echter niet per se dat de insectensoorten die van deze planten afhankelijk zijn er ook daarwerkelijk gebruik van kunnen maken, bijvoorbeeld omdat de benodigde structuren ontbreken, of juist omdat het microklimaat ongeschikt is (zie ook box 1 en 2). Een vierde mechanisme loopt via de bodem. Grote herbivoren oefenen druk uit op de bodem, waardoor deze verdicht kan raken. Onduidelijk was of dit effect zou hebben op bovengrondse fauna, en in hoofdstuk 5 hebben we hiervoor ook geen aanwijzingen gevonden. Het laatste, en eveneens weinig onderzochte aspect is de verandering in interacties tussen soorten ongewervelden. Het is geopperd dat grote herbivoren een verkorting van voedselketens kunnen veroorzaken doordat de minder abundante soorten hoog in de keten het eerste zullen verdwijnen, maar hiervoor is weinig experimenteel bewijs.

Aan de hand van dit mechanistische raamwerk blijkt dat natuurbeheer met behulp van grote herbivoren alleen positieve effecten op de soortenrijkdom van ongewervelden kan hebben als de gecreëerde heterogeniteit in vegetatietypen en plantensoorten groot genoeg is om de negatieve effecten teniet te doen. De kans om dit te bereiken is het grootst onder de volgende beheeropties: een mozaïek van verschillende beweidings regimes, onder beweiding met lage dichtheden, of onder rotatiebeheer met cycli van een jaar of meer.

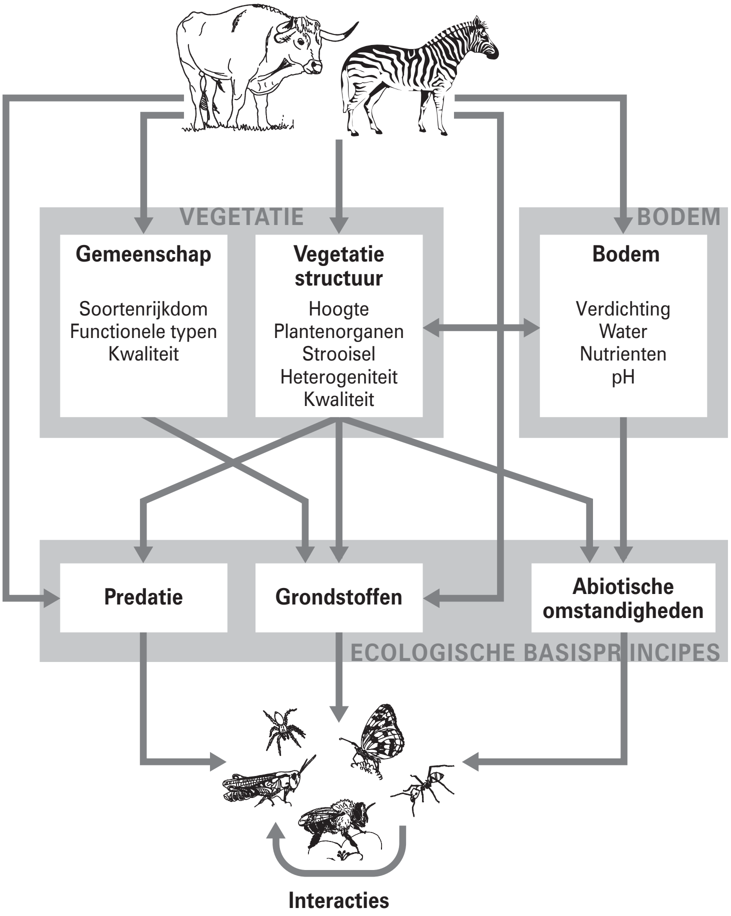

Figure 9.1 Conceptueel raamwerk van de mechanismen waardoor grote grazers op directe en indirecte wijze gemeenschappen van ongewervelden beinvloeden.

Effecten van beweiding op insecten en spinnen langs de overstromingsgradient van kwelders (hoofdstuk 3)

Om meer begrip te krijgen van de specifieke situatie op de kwelders heb ik bij aanvang van de beweidingsproef een vergelijking gemaakt tussen de gemeenschappen van drie groepen carnivore ongewervelden – spinnen, loopkevers en oeverwantsen – op beweide en onbeweide kwelders van Noord-Friesland Buitendijks en Schiermonnikoog langs de gehele overstromingsgradient. Ik verwachtte dat met een toename in overstromingsfrequentie een afname in soortenrijkdom en variatie in soortensamenstelling (β-diversiteit) zou plaatsvinden, omdat immers alleen de aangepaste soorten deze extreme omstandigheden kunnen overleven. Deze verwachting werd grotendeels bevestigd, maar verschilde tussen soorten die aan kwelders gebonden zijn en binnenlandse soorten. De soorten die niet specifiek aan kwelders gebonden zijn namen met een toename in overstromingsfrequentie inderdaad af in soortenrijkdom maar hun β-diversiteit nam toe, vooral op de beweide kwelder. De soorten die aan kwelders gebonden zijn lieten het tegenovergestelde patroon zien, en hadden de hoogste β-diversiteit op de lage, onbeweide kwelder terwijl hun soortenrijkdom niet veranderde. Variatie in soortensamenstelling bleek dus het hoogst te zijn onder gunstige omstandigheden en onder extreme omstandigheden. Wat onder gunstig en extreem moet worden verstaan bleek dus afhankelijk van de mate van specialisatie in de specifieke omstandigheden van de kwelder.

Lange termijn effecten van beweiding op insecten en spinnen (hoofdstuk 4)

Op drie kwelders in de Duitse deelstaat Sleeswijk-Holstein liggen al ruim 20 jaar beweidingsproeven met drie verschillende dichtheden schapen (onbeweid, matige dichtheid (4 schapen per hectare), hoge dichtheid (10 schapen per hectare)). Dit bood een kans om de langetermijneffecten van deze verschillende begrazingsintensiteiten te bestuderen.

Onder matige dichteden bleken de schapen stabiele mozaïeken van hoge en lage vegetatie te hebben gecreëerd doordat ze regelmatig terugkeren naar reeds afgegraasde vegetatie, waarvan de hergroei een hoge voedingswaarde heeft, en andere stukken links laten liggen. In tegenstelling tot de hierboven genoemde verwachting vond ik niet dat mozaïeken een hogere soortenrijkdom van ongewervelden herbergden dan de homogeen hoge, onbeweide vegetatie. Wel bevatten de mozaïeken veel meer soorten dan de de homogeen kort gegraasde vegetatie onder hoge dichtheden schapen. De meeste soorten insecten en spinnen bleken een duidelijke voorkeur te hebben voor òf hoge òf lage vegetatie, en slechts een klein deel van de soorten bereikte hoogste dichtheden in de vegetatiemozaïeken. Voor de soorten die aan kwelders gebonden zijn was dit vooral te danken was aan de hoge dichtheden van hun waardplanten Zeealsem (*Artermisia maritima*) en Zilte rus (*Juncus gerardii*), die door de schapen vermeden werden.

Het scheiden van de effecten van bodemverdichting en grazen (hoofdstuk 5)

Om inzicht te krijgen in de mechanismen waarmee grote herbivoren ecosystemen beïnvloeden heb ik samen met verschillende collega's een experiment opgezet om de afzonderlijke effecten van het afgrazen van vegetatie en verdichting van de bodem te ontrafelen. Hiertoe hebben we op de onbeweide kwelder van Noord-Friesland Buitendijks drie behandelingen uitgevoerd: bodemverdichting met behulp van een trilstamper (jaarlijks), maaien met een bosmaaier (maandelijks) en zowel maaien als verdichten. Dit hebben we vergeleken met een onbehandelde controle en met de langduring beweide kwelder (1 rund per ha) in het beweidingsexperiment.

Er bleken grote verschillen te bestaan in de effecten van onze behandelingen op planten, bodemfauna (mijten en springstaarten) en bovengrondse fauna (spinnen en kevers). De bovengrondse fauna reageerde alleen op de maaibehandeling, terwijl de bodemfaunagemeenschap vooral werd beïnvloed door bodemverdichting. De plantengemeenschap werd door beide behandelingen beïnvloed, hoewel het effect van maaien veel groter was dan het effect van bodemverdichting. In geen van de drie groepen was na behandeling de soortensamenstelling gelijk aan die van de beweide kwelder, hoewel vooral de plantengemeenschap wel een duidelijke trend in die richting liet zien. We concluderen dat op kwelders bodemverdichting een tot nu toe onderschatte bijdrage levert aan de effecten van grote herbivoren op de flora en fauna.

Bloembezoekende insecten onder verschillende beweidingsregimes

(hoofdstuk 6)

In het beweidingsexperiment aan de Friese vastelandskust heb ik onderzocht wat de effecten zijn van de verschillende beweidingsregimes op bloembezoekende insecten. Dit heb ik gedaan door langs transecten in elk proefveld zowel het bloemaanbod als de abundantie van bloembezoekende insecten (vlinders, hommels en zweefvliegen) te bepalen.

Paardenbeweiding met hoge dichtheden bleek desastreus voor zowel het bloemaanbod als de bloembezoekers. Positief voor de bloembezoekers waren beweiding met lage dichtheden paarden of koeien, en vooral ook de onbeweide jaren in het rotatiebeheer. De bepalende factor hiervoor bleek het aanbod aan bloemen te zijn, en in het bijzonder hoge composieten zoals Zulte (*Aster tripolium*), Akkerdistel (C*irsium arvense*) en Reukeloze kamille (*Tripleurospermum maritimum*). De hoeveelheid bloemen van deze plantensoorten in combinatie met jaareffecten verklaarde 90% van de variatie in aantallen bloembezoekers, en dit lijkt dus een sterke indicator voor de habitatkwaliteit voor bloembzoekers.

Het dieet en foerageergedrag van Graspiepers op beweide kwelders

(Hoofdstuk 7)

Insecten en spinnen vormen het voedsel voor veel vogelsoorten, maar worden zoals hierboven is gebleken sterk beïnvloed door grote herbivoren. We waren daarom geïnteresseerd in de keuze van dieet en fourageerlocaties van broedende Graspiepers (*Anthus pratensis*) op beweide kwelders.

Door analyse van de uitwerpselen van de kuikens bleek dat grotere spinnen (> 5 mm) en rupsen het belangrijkste voer van Graspieperkuikens op de kwelder vormen. Deze groepen waren aanzienlijk meer vertegenwoordigd in de uitwerpselen dan in de bemonsterde vegetatie, terwijl andere groepen zoals kleine kevertjes en spinnentjes (< 5 mm), die vaak zeer talrijk zijn op de kwelder niet werden gevonden in de uitwerpselen. We hadden verwacht dat graspiepers zouden foerageren op plekken met veel overgangen tussen hoge en lage vegetatie, zodat ze zich makkelijk kunnen voortbewegen in de korte vegetatie, terwijl hun prooien vooral in de hoge vegetatie zitten. Dit bleek echter niet het geval. We vonden dat Graspiepers foerageerden in relatief homogene vegetatie, maar vonden geen verschil in vegetatiehoogte tussen de foerageerlocatie en controleplekken. Dit laat zien dat het ontstaan van een mozaïek van hoge en lage vegetatie niet per se positief hoeft te zijn voor alle soorten, maar duidlijk is ook dat meer onderzoek nodig is naar de eigenschappen van de vegetatiemozaïeken en hun belang voor vogels en hun prooi.

Het belang van waardplantconditie en microklimaat voor herbivore insecten

(Box 1 & 2)

Om te begrijpen hoe herbivore insecten reageren op de modificatie van hun waardplant en microclimaat is in de beweidingsproef op de kwelders van Noord-Friesland Buitendijks gekeken naar de effecten van beweiding op de insecten die leven op Zulte (*Aster tripolium*). Hier bleek het rotatiebeheer tijdens onbeweide jaren wederom erg positief, omdat er per plant meer soorten insecten voorkwamen dan onder zowel runderbeweiding als zonder beweiding. De verklaring hiervoor bleek vooral te liggen in het gewicht van de plant, dat goed correleerde met het aantal bloemen en de grootte van de plant.

Om te kijken in hoeverre deze resultaten ook gelden voor andere planten heb ik een experiment uitgevoerd met manipulatie van biomassa (knippen) en microklimaat (beschaduwing) van vijf kwelderplanten: Zulte, Zeealsem, Zeeweegbree (*Plantago maritima*), Kweldergras (*Puccinellia maritima*) en Rood Zwenkgras (*Festuca rubra*). Voor Zulte bleek wederom de grootte van de plant de belangrijkste verklarende factor voor de dichtheid aan herbivore insecten, en de grootte werd vooral bepaald door de knipbehandeling. Voor Zeealsem waren er ook sterke aanwijzingen dat de grootte van belang was, maar deze werd vooral bepaald door beschaduwing door de omringende vegetatie. Tijdens de vestiging van deze plant is voldoende licht van belang, maar de volwassen planten zijn relatief goed bestand tegen overwoekering door hoge grassen (zie ook hoofdstuk 4). De fauna van Gewoon kweldergras en Rood zwenkgras daarentegen werd nauwelijks beïnvloed door de grootte van de plant, maar des temeer door het microklimaat. Er waren dan ook meer insecten per plant op de planten die niet in de schaduw van de omringende vegetatie stonden. Op Zeeweegbree werden om onduidelijke redenen helemaal geen insecten gevonden, ondanks het feit dat deze soorten wel op deze kwelder aanwezig waren.

Conclusies voor het beheer van kwelders (Hoofdstuk 8)

Het doel van natuurbeheer op kwelders dient het behoud te zijn van alle soorten planten, ongewervelden en gewervelden die aan kwelders gebonden zijn. Omdat mijn onderzoek heeft duidelijk gemaakt dat het onwaarschijnlijk is dat alle soorten in hun behoeften kunnen worden voorzien binnen één beheervorm (zie Box 3 voor een lijst van aan kwelders gebonden soorten en hun respons op beheer), zal het nodig zijn om zowel beweide als onbeweide kwelders naast elkaar te behouden. Het is daarin van belang om vast te stellen hoe die beweiding het beste plaats kan vinden. Hieronder bespreek ik de effecten van verschillende beheerkeuzes.

Stoppen met beweiding zal tot gevolg hebben dat grote delen van de kwelder worden gedomineerd door Zeekweek. Slechts enkele plekken met slechte afwatering zullen niet worden gedomineerd, maar deze bieden wel zeer gunstige mogelijkheden voor veel soorten ongewervelden. Ook in de door Zeekweek gedomineerde vegetatie kunnen veel soorten voorkomen, maar kleine waardplanten en hun fauna zullen verdwijnen, en het is onduidelijk of dit proces omkeerbaar is. Beweiding is dan ook nodig om deze soorten plaats te bieden.

Er is weinig bewijs dat de keuze van het soort vee dat gebruikt wordt bij beweiding van belang is voor ongewervelden, ondanks aangetoonde verschillen in activiteit en dieet (zie Mandema 2014, Nolte 2014). Omdat de paarden gebruikt in het onderzoek op de Friese kwelders zwaarder waren, en ongeveer 1.7 maal zo veel tijd per dag besteedden aan grazen als de runderen (Nolte 2014) is het waarschijnlijk dat gevonden verschillen tussen paarden en runderbeweiding (zie vooral Fig. 8.2) grotendeels te wijten zijn aan dit verschil in biomassa per hectare. Wel vertrappen paarden veel meer dan runderen, en daarom zou paardenbeweiding ook na correctie voor verschil in gewicht en voedselopname een negatiever effect op ongewervelden en ook vogels kunnen hebben.

Keuze van de beweidingsdichtheid, daarentegen, heeft grote gevolgen voor ongewervelden. Terwijl beweiding met hoge veedichtheden geen waarde heeft voor de bescherming van ongewervelden, heeft beweiding met matige dichtheden positieve effecten, vooral op de fauna van de planten die gemeden worden. Bij beweiding met lage dichtheden zullen veel soorten ongewervelden profiteren, maar zal Zeekweek waarschijnlijk wel uitbreiden.

Rotatiebeheer is in mijn onderzoek als veelbelovende beheervariant naar boven gekomen, hoewel de langetermijneffecten nog niet goed bekend zijn. Tijdens onbeweide jaren krijgen gevoelige plant- en diersoorten de mogelijkheid om grote populaties op te bouwen, wat ze kan bufferen tegen de ongunstiger omstandigheden tijdens beweide jaren. Voor soorten die baat hebben bij beweiding geldt het omgekeerde. Bij de keus van beweidingsdichtheid gedurende beweide jaren zal rekening moeten worden gehouden met sterk negatieve effecten van hoge dichtheden, en het is aan te bevelen om niet de hoogste dichtheden te gebruiken, omdat veel populaties dat niet zullen overleven. Mijn persoonlijke inschatting is dat één rund per hectare waarschijnlijk geen negatieve gevolgen heeft, maar dezelfde dichtheid aan paarden hoogstwaarschijnlijk wel, vanwege de vertrapping. Ook is het waarschijnlijk dat Zeekweek een zekere uitbreiding zal laten zien, maar dat heeft waarschijnlijk positieve effecten op veel soorten ongewervelden.

Monitoring van ongewervelden

Wanneer beheer wordt uitgevoerd is het van belang om de effecten van dit beheer op de doelsoorten te volgen. Omdat voor het monitoren van gemeenschappen van ongewervelden veel tijd en expertise nodig zijn, is het voor beheerders van belang om makkelijk meetbare indicatoren te kunnen volgen. Uit mijn onderzoek zijn enkele betrouwbare indicatoren voor de habitatkwaliteit voor een aantal soorten ongewervelden naar voren gekomen:

- Voor ongewervelden die afhankelijk zijn van voor vee slecht eetbare waardplanten (Zeealsem, Zeerus en onder schapenbeweiding ook Zilte rus) is het bedekkingspercentage van volwassen planten een goede indicator van hun rijkdom aan insecten. Voor veel andere plantensoorten, en in het bijzonder grassen, is bedekkingspercentage een slechte voorspeller van de soorten die erop kunnen voorkomen.
- Voor bloembezoekers en de soorten die leven van Zulte is het aantal bloemen een betrouwbare indicator voor hun dichtheden. Het aantal bloemen per plant correleert sterk met het aantal insecten dat er op kan leven, en het aantal bloemen (geschat in abundantieklassen) per beheereenheid is een betrouwbare indicator van het aantal bloembezoekers dat erop kan leven. Op kwelders waar andere belangrijke nectarbronnen zoals Lamsoor (*Limonium vulgare*) en Engels Gras (*Armeria maritima*) voorkomen zal het belang van deze soorten voor bloembezoekers eerst onderzocht moeten worden.

Samengevatte aanbevelingen voor bescherming van ongewervelden op kwelders

- **Beweiding met hoge dichtheden herbivoren** (1 paard / ca. 1.5 rund / 10 schapen ha^{-1}) **heeft geen waarde voor de bescherming van ongewervelden**.
- **Onbeweide kwelders**, zelfs die gedomineerd worden door Zeekweek of Zoutmelde (*Atriplex portulacoides*) **hebben waarde voor ongewervelden**, zoals het endemische Klokspinnetje (*Praestigia duffeyi*) dat alleen voorkomt op onbeweide lage kwelders.
- Er zijn veel aanwijzingen dat het **stoppen van beweiding voor korte perioden, zoals bij rotatiebeheer, erg positief is voor ongewervelden**. De periode waarin de kwelder onbeweid blijft kan meerdere jaren duren, maar hierbij moet worden bedacht dat zodra er plantensoorten verdwijnen, hun geassocieerde fauna ook zal verdwijnen. Ook moet men er rekening mee houden dat zodra beweiding wordt hervat de beweidingsdichtheid zal bepalen of en welke van de opgebouwde populaties kunnen overleven.
- Onder **beweiding met matige dichtheden** (0.5 paard / 1 rund / 3-4 schapen ha^{-1}) zal een mozaïek van hoge en lage vegetatie ontstaan **waarvan voor vee slecht eetbare plantensoorten** zoals Zeealsem en Russen **en hun fauna kunnen profiteren**.
- Beweiding met lage dichtheden (0.5 koe / 1-3 schapen ha^{-1}) kan positief zijn voor door vee geprefereerde plantensoorten zoals Zulte, maar geeft wel ruimte aan de uitbreiding van Zeekweek.
- **Mijn aanbeveling is dat deze laatste vier beheeropties ten alle tijden op de kwelder aanwezig moeten zijn** zodat de mogelijkheden voor alle doelsoorten gemaximaliseerd worden. Een mozaïek van beheervormen met een onderlinge rotatie over een periode van tientallen jaren zou de bescherming van kweldersoorten moeten waarborgen.

VERVOLGONDERZOEK

Er is nog veel onbekend over het beheren van kwelders voor planten, vogels, en vooral ongewervelden. Het eerste en belangrijkste aspect dat meer aandacht verdient zijn de langetermijneffecten van de verschillende beheervormen op de Friese kwelders. In het bijzonder zal het van belang zijn te onderzoeken wat de effecten van het veelbelovende rotatiebeheer zullen zijn op de lange termijn.

Ten tweede heb ik slechts de effecten op een beperkte groep ongewervelden kunnen onderzoeken, terwijl enkele zeer soortenrijke groepen buiten beschouwing zijn gebleven: vliegen en parasitaire wespen. Het is een zware opgave om deze soorten bij beheer te betrekken.

Ten derde zal het zeer belangrijk zijn om goede indicatoren voor de habitatkwaliteit voor ongewervelden te ontwikkelen. Mijn onderzoek heeft enkele indicatoren opgeleverd, maar voor de meerderheid van de soorten zijn die nog niet voorhanden. De lijst van doelsoorten en hun globale respons op beheer, gepresenteerd in box 3, kan hiervoor handvatten bieden.

Ten slotte is het nodig om de habitateisen van een aantal zeldzame aan kwelders gebonden soorten vast te stellen. Het gaat hier bijvoorbeeld om de zeldzame loopkever Zilte Bontloper (*Acupalpus elegans*) en de nachtvlinders Kwelderpistoolmot (*Aristotelia brizella*) en het Schorzandvleugeltje (*Scrobipalpa samadensis*), die zich respectievelijk voeden met de juist niet zeldzame kweldersoorten Engels gras en Zeeweegbree. Het kennen van de habitateisen van deze soorten zal hun bescherming ten goede komen.

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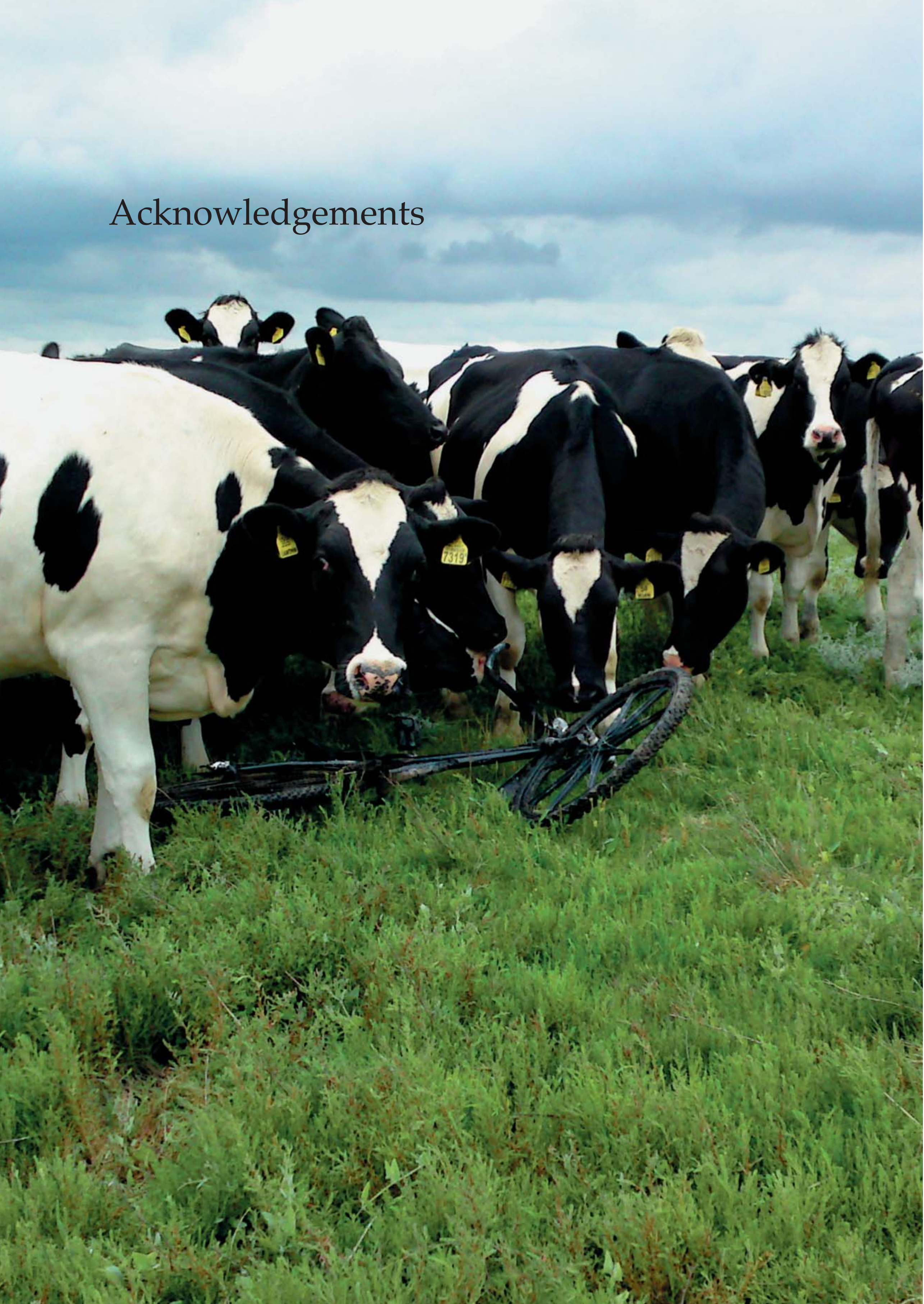

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Now it's time to get back to work. I am very much looking forward to future projects, forging new collaborations, starting new projects, writing new papers and working on new ideas about the workings of the natural world. Time is running out.

List of publications

Schrama, M.; **Van Klink, R.** (in press) Effects of large mammalian grazers on soil biodiversity *in*: World atlas of soil biodiversity. Six, J. ed.

Van Klink, R.; van der Plas, F.; van Noordwijk, C.G.E. (Toos); WallisDeVries, M.F.; Olff, H. 2014. Effects of large herbivores on arthropod diversity. Biological Reviews in press

Van Klink, R.; Mandema, F.S.; Bakker, J.P.; Tinbergen, J.M. 2014. Foraging site choice and diet selection of Meadow Pipits *Anthus pratensis* breeding on grazed salt marshes. Bird Study 61: 101-110

De Vlas, J.; Mandema, F.; Nolte, S.; **Van Klink, R.**; Esselink, P.E. 2013. Nature conservation of salt marshes – the influence of grazing on biodiversity, It Fryske Gea, Oldertерp, The Netherlands

Van Klink, R.; Rickert, C.; Vermeulen, R.; Vorst, O.; WallisDeVries, M.F.; Bakker, J.P. 2013. Grazed vegetation mosaics do not maximize arthropod diversity: Evidence from salt marshes. Biological Conservation 164: 150-157

Thasing, S.; **Van Klink, R.**; Schepers, M; Cappers, R.T.J.; Brüning, E.B.E. 2012. Kevers en hun potentie voor onderzoek in het terpengebied. Paleo-aktueel 23: 111-118

Rickert, C.; Fichtner, A.; **Van Klink, R.**; Bakker, J.P. 2012. Alpha- and beta-diversity in moth communities in salt marshes is driven by grazing management. Biological Conservation 146, 24-31

Kohler, F.; Verhulst, J.; **Van Klink, R.**; Kleijn, D. (2008). At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? Journal of Applied Ecology 45: 753-762

Kohler, F.; **Van Klink, R.**; Noordijk, J. (2007). De invloed van natuurgebieden op zweefvliegen en bijen in agrarische gebieden (Diptera: Syrphidae; Hymenoptera: Apidae) Entomologische Berichten 67: 187-192

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Always against the odds - One with the underdogs