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Through arthropod eyes

Gaining mechanistic understanding of
calcareous grassland diversity



Toos van Noordwijk

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Through arthropod eyes

Gaining mechanistic understanding of calcareous grassland diversity

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Marijn Nijssen

Wilco Verberk

Every kid has a bug period... I never grew out of mine.

E.O. Wilson

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Installing pitfall traps just before a thundery spring shower (Photo: Toos van Noordwijk)



Chapter 1

General introduction

C.G.E. (Toos) van Noordwijk

Challenges in conservation ecology

Over the past century, a multitude of anthropogenic stressors, including land-use change, eutrophication, fragmentation and climate change, have led to large-scale biodiversity declines (Millennium Ecosystem Assessment 2005). International conventions to halt biodiversity loss have led to the development of stringent policy to protect and manage (semi-)natural habitats. Prominent examples are the European Commission's Habitats Directive and the subsequent formulation of the Natura 2000 network. A major challenge in conservation ecology is to devise practical strategies to turn these paper promises into reality.

In semi-natural habitats like calcareous grasslands, which were formed over the centuries through low-intensity farming practices, the initial conservation response generally is to revert back to these traditional farming practices (Ostermann 1998). However, for a number of reasons this may not be the best option. Firstly, due to sharp increases in the costs of manual labour and drastic changes to farming practices, exactly copying traditional methods is seldom feasible for economical, practical and social reasons. Partially implementing traditional methods, e.g. reintroducing hay making, but executing it mechanically over large areas at once, may do more harm than good (e.g. Konvicka et al. 2008). Secondly, nutrient-cycles in semi-natural habitats, have changed dramatically with the arrival of artificial fertilizers (Bobbink et al. 1998; Bakker and Berendse 1999; Stevens et al. 2004). Traditional farming practices are likely to be insufficient to keep up with aerial nitrogen deposition, let alone with the nutrient enrichment that has built up in the soil during years of abandonment. Thirdly, in addition to factors operating within nature reserves, the landscape context has changed dramatically as well. Where semi-natural habitats once covered large parts of the agricultural landscape, they are now often reduced to small habitat fragments surrounded by intensively managed arable land, which is uninhabitable for the majority of plant and animal species (Benton et al. 2002; Kerr and Cihlar 2004; Green et al. 2005). This fragmentation and habitat isolation cause populations to be smaller and more isolated, putting them at greater risk of local extinction (MacArthur and Wilson 1967; Hanski 1999). Even if habitat quality has been restored successfully, habitat fragmentation and isolation still form a major constraint for biodiversity conservation (Tilman et al. 1994; Huxel and Hastings 1999; Ozinga et al. 2005).

To adequately address all of these issues we thus need to design new conservation strategies that are effective in dealing with current environmental pressures and are practically, economically and socially feasible. This requires first and foremost, thorough understanding of the mechanisms shaping biodiversity in semi-natural habitats. Such mechanistic understanding of semi-natural ecosystems has grown over the years, but has to date focussed primarily on plants (WallisDeVries et al. 2002; Littlewood et al. 2012). Arthropods have received far less attention, despite being the most species-rich eukaryotic group on earth and performing many essential functions within ecosystems, including nutrient-cycling and pollination (Littlewood et al. 2012; Prather et al. 2013). Evidence is mounting that the response of arthropods to environmental stressors and conservation management differs crucially from plants (e.g. Morris 2000; Kruess and Tscharntke 2002a; WallisDeVries et al. 2002; Littlewood et al. 2012). Therefore, it is imperative to understand the specific mechanisms shaping arthropod communities.

Identifying main bottlenecks for conservation

Community ecology has traditionally either focussed on the interactions between single pairs of species or taken a correlative approach to species-environment relationships (McGill et al. 2006) (Figure 1a). Species communities are often reduced to simple metrics like richness, abundance or dissimilarity and are correlated to one or multiple environmental factors. Alternatively, multivariate techniques are used to link the dominant pattern of variation in community composition to environmental gradients. Such approaches are valuable to accurately describe differences between localities in space or time and may be used to explore which factors, out of the multitude of measured ones, are associated with the observed differences in species occurrences. However, when it comes to finding the underlying mechanisms, they present two major problems. Firstly, correlation does not automatically imply a direct causal relationship (Weiner 1995; Michener 1997; Shipley 2004). Causal understanding is essential to predict which actions will be most effective

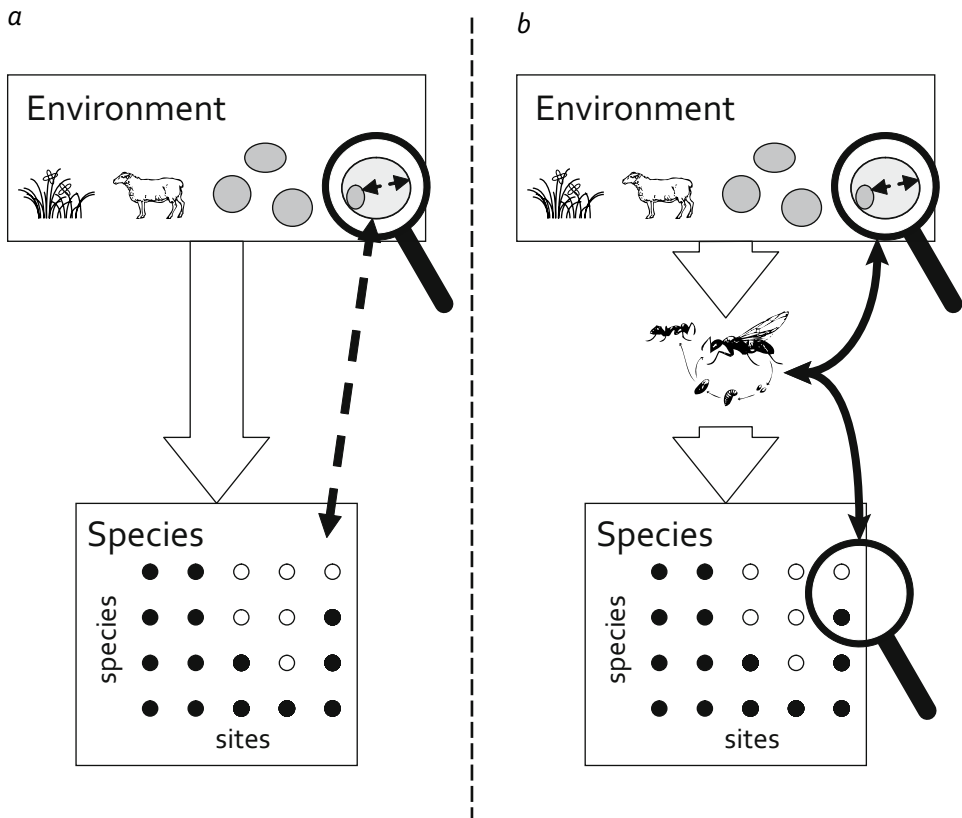


Figure 1. Environmental factors like (from left to right) vegetation structure, management regime, habitat fragmentation and habitat area, affect arthropod communities. (a) Species-environment relationships are traditionally inferred from correlations (dashed black arrow) often between one or more environmental factor(s) and community metrics like species richness or (dis)similarity. (b) Trait-based methods aim to unravel the causal mechanism behind species-environment relationships (solid black arrows), by focusing on which species are affected and exploring how the environment affects their life cycles.

for reaching conservation goals (Bradshaw 1996; Hobbs and Norton 1996). When environmental factors are correlated, which is often the case in conservation ecology (e.g. correlations between habitat area and the influence of edge-effects or between vegetation structure, microclimate and disturbance from management), it is impossible to establish the relative importance of each single factor with purely correlative studies. Secondly, when linking environmental factors to community metrics researchers generally include a limited set of standard parameters. Especially in complex restoration situations, the number of possible factors to measure is overwhelming. Many factors like microclimate, fragmentation and management practice can be measured in different ways and at different levels of detail, all with a (slightly) different outcome as a result. Selecting which factors to measure without understanding of how species use their environment can obscure important relationships and prevents the discovery of new key factors. This limits the value of applied restoration and conservation ecology to advance our understanding regarding more fundamental aspects of community ecology. To circumvent these problems, research is increasingly focussing on species' traits (Calow 1987; Keddy 1992; McGill et al. 2006; Violle et al. 2007) (Figure 1b). By making explicit which species respond in a particular way to environmental change and by analysing their traits, causal links can be established.

The habitat as a filter

The idea that the ecology of species can be used to unravel species-environment relationships stems from Southwood's habitat templet theory (1977). This theory states that the habitat provides the templet on which evolution forges characteristic life-history strategies. As these strategies are 'designed' (by natural selection) to increase fitness in a specific habitat, they can be used to understand how the habitat 'filters' the regional species pool to form the local community (Keddy 1992; Poff 1997; Webb et al. 2010). In this filter concept three types of filters have been distinguished (Figure 2). First a dispersal filter determines which species actually reach the local site. These species are then filtered by a set of environmental filters (e.g. relating to microclimate and site size). Species must be able to cope with all these filters to be able to persist in the local community. Finally, there is a limiting similarity filter, which excludes species that are too strongly alike, as they will experience fierce competition. This causes selection against co-occurrence of such very similar species.

The dispersal and environmental filters thus select for species whose life-history strategy leads to occurrence under similar environmental conditions (Verberk et al. 2013). Such groups of species that respond similarly to their environment have been called life-history strategies or tactics (Siepel 1994; Verberk 2008). The relative abundance of different strategies in a specific site depends on the filters that operate on it (see Figure 2). This implies that the species composition of a site, combined with knowledge on species' life-history strategies, can be used to deduce which environmental factors (i.e. filters) act on that site.

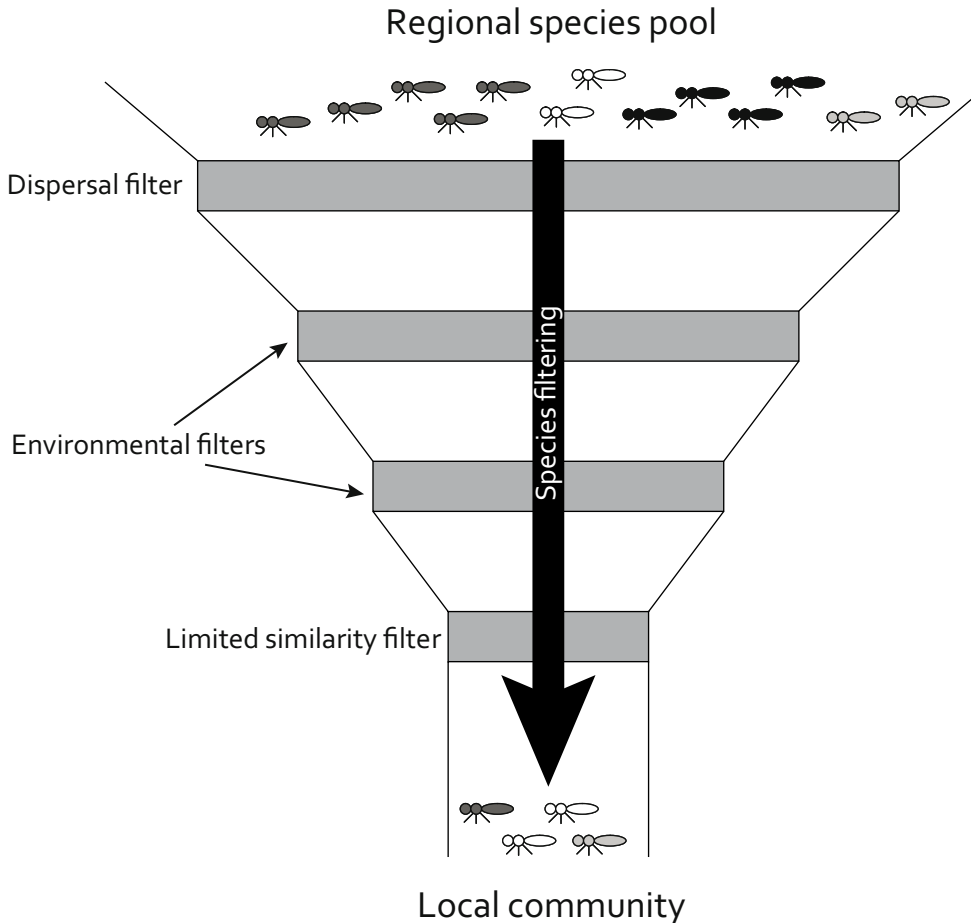


Figure 2. Species from the regional species pool are filtered non-randomly by a dispersal filter, environmental filters (e.g. microclimate and site size) and a limited similarity filter to form the local species pool. The dispersal filter and the environmental filters select for species that respond in a similar way to their environment, i.e. have the same life-history strategy (represented by the same shade of grey). The limiting similarity filter selects for species with different life-history strategies. This leads to a local community in which the relative abundance of life-history strategies (compared to the regional species pool) differs depending on their match with the operating filters.

Traits

How species respond to their environment depends on their life-history strategy, which is formed by the combined effect of their traits (Stearns 1976). Traits in this sense are most commonly defined as any morphological, physiological or phenological feature which can be measured at the individual level without reference to the environment (Violle et al. 2007). This definition has a number of important consequences. Firstly, it states that traits are only those features that can be measured independent of the environment. It therefore excludes general ecological qualifications referring to preferences such as thermophilous (thriving best under warm conditions), xerophilous

(thriving best under dry conditions) or characteristic calcareous grassland species. These preferences are in effect the species-environment relationships for which we want to find the causal mechanisms and should thus be viewed separate from the underlying traits (Verberk et al. 2013). Secondly, traits in this definition only apply to the individual level. This is in line with the fact that natural selection, which drives the adaptation of a species to its environment, acts at the individual level. However, the relationship we set out to investigate is not between the environment and individual fitness, but rather between the environment and the occurrence of species (Figure 3). Most traits at the individual level can be translated to the species level, but an important additional feature is intraspecific variation within a population. This variation is in itself an important part of a species'

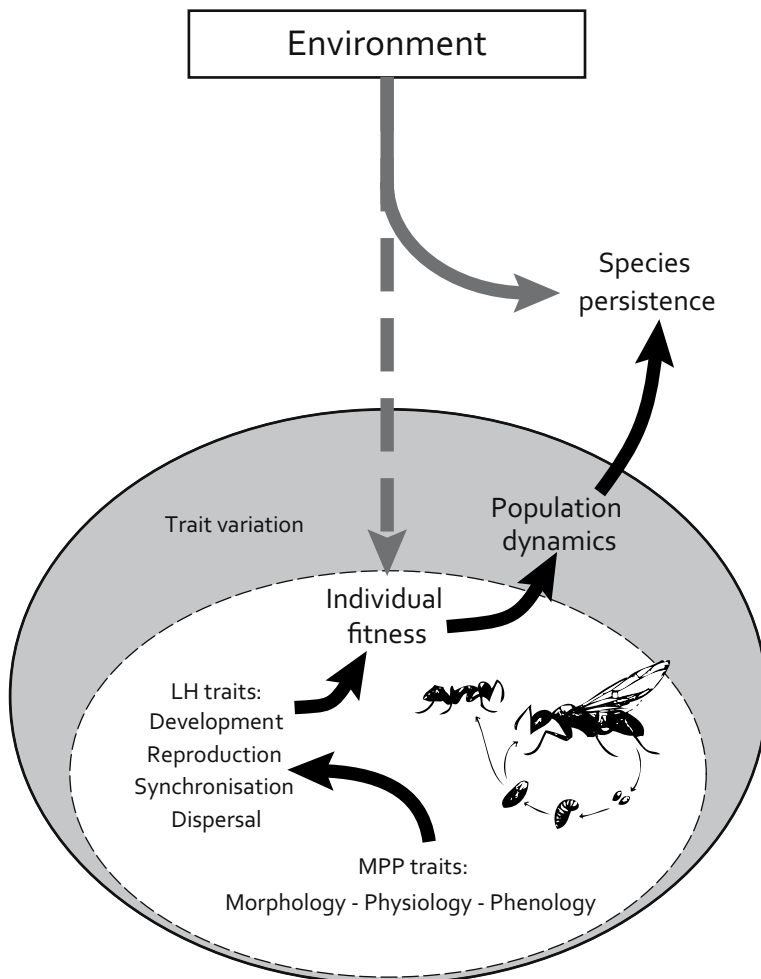


Figure 3. Ecological research aims to understand species-environment relationships (solid grey arrow). However, the environment does not affect species directly, but rather affects an individual's fitness (dashed grey arrow) throughout its life-cycle, based on the combination of traits possessed (i.e. its life-history strategy). Within an individual, traits operate at different levels, with morphological, phenological and physiological (MPP) traits underlying life-history (LH) traits. Trait variation at the population level affects population dynamics, which in turn determines species persistence.

Box 1. Trait definition

In this thesis traits are defined as any feature at the individual level that can be measured independent of the environment. This definition includes both morphological, phenological and physiological traits (MPP traits) and life-history traits (LH traits) related to reproduction, development, synchronisation and dispersal. Traits are principally measured at the individual level, but can be translated to the species level by incorporating variation in trait attributes (the value of a trait) within a population. This definition of traits explicitly excludes any preferences with respect to the habitat or other parts of the environment (e.g. habitat affinity or qualifications like thermophilous or xerophilous). Such environment-related features are referred to as 'characteristics' in this thesis

life-history strategy (Stearns 1976; Siepel 1994) and should thus be incorporated in our trait approach (see Figure 3). Thirdly, the definition given by Violle et al. (2007), if applied strictly, incorporates only morphological, phenological and physiological (MPP) traits. This is the most basic level of an individual's features, but it cannot be linked directly to fitness. MPP traits rather govern an individual's life-history, which in turn affects its fitness (Arnold 1983; Violle et al. 2007). The life-history responses have frequently been termed traits as well, even by Violle et al. (2007) themselves. In this thesis I largely follow Violle's trait definition, but extending it to include 1) mean trait values and trait variation at the species level and 2) an individual's life-history features, especially those associated with reproduction, development, synchronisation and dispersal (see Box 1). Thus, in line with Violle et al. (2007) I explicitly exclude any preferences with respect to the habitat or other parts of the environment. To make a clear distinction I use the term 'characteristics' for these external features rather than the commonly used term 'ecological traits'.

Using traits to predict responses

Research into the link between species and their environment to date, has strongly focussed on general trait-environment relationships (Keddy 1992, see also Verberk et al. 2013). However, traits have not been selected independently. Natural selection acts at the individual level and an individual's fitness is determined by the combined effect of its traits. Life-history strategy theory, including Southwoods habitat template theory that sparked greater interest in trait research in the first place, indeed predicts that within species, traits are linked to form an integrated response to particular ecological problems (Stearns 1976; Southwood 1977; Siepel 1994). Traits are interconnected through trade-offs and different traits may act in concert (Siepel 1994; Van Kleef et al. 2006; Verberk et al. 2008a). Investments in one trait may have repercussions for investments in another (e.g. species generally lay either few large eggs or many small eggs but not many large eggs). Also, a specific trait may have different ecological implications depending on the remainder of the traits possessed by the species and different combinations of traits may be functionally equivalent. An example of such trait interactions and context dependence is the effect of body-size on a species' dispersal ability. Body size has been found to be positively related to a species' ability to reach isolated sites in bees (Steffan-Dewenter and Tscharnkte 1999). However, in carabid beetles, there appears to be a trait interaction between body size and flight ability, with large species all being wingless (Turin 2000). As flight ability has a strong

positive effect on a species' ability to reach isolated sites, larger bodied carabid species can be assumed to be more instead of less vulnerable to habitat isolation, since they cannot fly. Larger species can however, run faster than small species. Thus within the non-flying carabids, larger bodied species will be better at colonising isolated habitats (Gutierrez and Menendez 1997). Thus, while there does not seem to be an overall relationship between body size and the ability to cope with habitat isolation in carabid beetles, body-size does actually affect a species' performance, but this depends on its flight ability. Due to such context-dependence of trait values it is essential to incorporate trait interactions in the study of species-environment relationships (Verberk et al. 2013).

Study system: Calcareous grasslands

Using traits and their interactions to unravel species-environment relationships has the potential to provide the mechanistic understanding that is needed to design new conservation strategies that address contemporary environmental pressures. In this thesis, I investigate this issue using a case-study on arthropods in calcareous grasslands.

Calcareous grasslands are nutrient-poor grasslands on base-rich soils. They are very rich in arthropods from many different taxonomic groups (Lindroth 1949; McLean et al. 1990; Morris et al. 1990; Van Swaay 2002; WallisDeVries et al. 2002; Dekoninck et al. 2007), due to their extraordinary plant species richness, unique microclimate and potentially varied vegetation structure (see Box 2). Over the past century, the number, size and quality of calcareous grasslands in North-Western Europe have declined strongly (Bobbink and Willems 2001; Poschlod and WallisDeVries 2002; WallisDeVries et al. 2002). Agricultural intensification and the introduction of artificial fertilizers have led to abandonment of the original farming practices, like low intensity sheep grazing, that originally shaped these grasslands (Willems 2001; Poschlod and WallisDeVries 2002). Calcareous grasslands were converted to arable land and strongly improved (fertilized) agricultural grassland (Baldock et al. 1996), which resulted in a strong decline in plant and arthropod richness (WallisDeVries et al. 2002). In the Netherlands only 20 calcareous grassland sites remained with a combined surface area of no more than 30 ha. (see Box 3). Remaining sites became increasingly fragmented and isolated and absence of management led to severe grass, shrub and tree encroachment, causing plant and arthropod species richness to decline even further (Willems 2001; WallisDeVries et al. 2002; Dover et al. 2011). In many sites, the problems caused by fragmentation and abandonment were further amplified by eutrophication from both adjacent agricultural areas (run-off) and airborne nitrogen pollution (Bobbink and Willems 1993; Willems 2001).

To counter the negative effects of abandonment on calcareous grassland biodiversity, remaining sites across Europe are increasingly managed for nature conservation purposes (Ostermann 1998) or included in agri-environment schemes (WallisDeVries et al. 2007; Konvicka et al. 2008). Conservation management usually focuses on removing excess primary production with the aim of enhancing plant species richness (Bobbink and Willems 1993; Kahmen et al. 2002; WallisDeVries et al. 2002). The main management methods are mowing or grazing with large herbivores (predominantly sheep). Although management is essential to prevent encroachment of tall grasses, shrubs and trees,

Box 2. Why are calcareous grasslands so rich in arthropods?

Several features make calcareous grasslands especially suitable for a wide range of (specialist) arthropod species. Firstly, calcareous grasslands are extraordinarily rich in plant species (Peet et al. 1983; Willems et al. 1993), which provides a large number of niches for specialist plant-feeders, including pollinators, sap-feeders and root feeders (Waloff 1980; Mortimer et al. 2002; WallisDeVries et al. 2002). This diversity of phytophagous species in turn supports a diverse community of carnivorous arthropods and parasitoids (Waloff 1980; Steffan-Dewenter and Tschamntke 2002).

Secondly, calcareous grasslands have a unique, warm microclimate. Most calcareous grasslands are found on slopes and calcareous soils drain relatively well, causing these grasslands to be dry. These dry conditions, combined with the low nutrient levels and thin organic soil layer typically found in calcareous grasslands, inhibits plant growth and leads to an open vegetation structure (Bobbink and Willems 2001). This open vegetation structure allows solar radiation to reach the ground. Calcareous soils have an excellent heat absorption and retention capacity (Stoutjesdijk and Barkman 1992), creating a warm microclimate. The effect of these soil properties are further enhanced on steep slopes with a southern aspect, due to their greater exposure to solar radiation (Stoutjesdijk and Barkman 1992). Although calcareous grasslands are relatively dry, calcareous soils retain more moisture than sandy soils, because of their smaller particle size, which makes them considerably moister underground than warm habitats found on sandy soils (heathlands, dune meadows etc.). In an extensive study Lindroth (1949) found that these microclimatic effects are the main reason for the strong affiliation of a significant number of carabid beetle species to calcareous grasslands. As arthropods are ectotherms, the warm and not extremely dry microclimate speeds up their development, enabling species with slower life-cycles to survive here. As such, calcareous grasslands in North-Western Europe provide suitable habitat for many species that are otherwise restricted to a more southern and eastern distribution range (e.g. Turin 2000; van Swaay 2002).

A third factor that greatly contributes to arthropod species richness in calcareous grasslands is the vegetation structure (Brown et al. 1990; McLean et al. 1990; Morris 2000). Depending on the management regime, the vegetation structure can be very heterogeneous with bare patches, short turf, higher stands of grassland vegetation and occasional trees and bushes all contained within a small area. This is especially the case in sites with small scale (few meters) variation in soil composition, aspect and inclination, as can be found in most Dutch calcareous grassland sites. The varied vegetation structure provides various food resources, structures (e.g. for egg-deposition) and hiding places (McLean et al. 1990; Morris et al. 1990; Morris 2000). In addition, higher stands of vegetation provide a moister and cooler microclimate than bare soil, providing a large gradient of microclimatic conditions on a small scale (Stoutjesdijk and Barkman 1992). This provides suitable conditions for a wide range of species, including species that need different conditions during different stages of their life-cycle.

renewed conservation management frequently does not yield the anticipated biodiversity recovery, especially for arthropods (WallisDeVries et al. 2002; Konvicka et al. 2008). Unravelling the causes of this lack of improvement is essential to conserve and restore arthropod biodiversity.

Box 3. Calcareous grasslands in Zuid-Limburg

In the Netherlands calcareous grasslands only occur on the lime-rich slopes of Zuid-Limburg. Here, they are often found in a gradient of vegetation types (especially in the western part of Zuid-Limburg). On the plateaus the calcareous soil is covered by a thick layer of loess. These areas are generally used for intensive agriculture and are heavily fertilized. The higher parts of the slopes often consist of sand and gravel deposits leading to acid grassland vegetations (Thero-Arion communities). Calcareous grasslands (*Mesobromion erecti*) are found on calcareous outcrops, which are usually situated halfway down the slope. Where gravel deposits and calcareous outcrops meet, matgrass swards (*Nardo-Galion saxatilis*) have developed. At the bottom of the slopes alluvial deposits have accumulated, leading to more nutrient-rich *Arrhenaterion elatioris* and *Arction* grasslands. This gradient in vegetation types is accompanied by a gradient in soil pH (ranging from 5.0 on acid gravel deposits to 8.0 on calcareous soils) and microclimate (from warm and dry via warm and slightly moister to cool and wet) (Bobbink and Willems 2001; Smits 2010). The occurrence of Dutch calcareous grasslands in this gradient undoubtedly adds to the local species richness and contributes to the value of Dutch calcareous grasslands in an international context (Bobbink and Willems 2001; Knol and Schaminée 2004).

The calcareous grasslands of Zuid-Limburg have attracted great botanical interest and their species composition has been well documented since the early twentieth century (e.g. Diemont and Van de Ven 1953). Faunistic records from the first half of the 20th century remain more anecdotal, but revealed nonetheless that these sites were very species rich. Many specialist arthropods could exclusively be found on calcareous grasslands within the Netherlands, including the carabid beetles *Callistus lunatus*, *Brachinus crepitans* and *B. explodens* (Turin 2000) and the butterflies *Spiralia sertorius* and *Thymelicus action* (Van der Made 1983) to name but a few.

Once, calcareous grasslands covered nearly fifty percent of the steep slopes in Zuid-Limburg (Bobbink and Willems 2001). They were used as common grazing grounds and formed an important part of the agricultural system. Manure from the grazing sheep was collected and used to fertilize the crop fields (Hillegers 1993). This active removal of nutrients over the centuries greatly contributed to the nutrient-poor state of the calcareous grasslands. With the introduction of artificial fertilizers and cheap Australian wool and later cotton, the traditional farming practice was no longer economically feasible (Hillegers 1993). Many calcareous grasslands were converted to arable land and remaining sites were left unmanaged (Willems 2001). Although recognition of the unique biotic value of calcareous grasslands came as early as 1942, with the formal protection of the Bemelerberg, systematic nature conservation management was not introduced until the late 1970ies (Hillegers 1984). By that time only 20 calcareous grassland sites remained with a combined surface area of no more than 30 ha. (Willems 2001). Extensive pitfall sampling campaigns in 1977 and 1981 revealed that only few sites still had a characteristic xero-thermophilic (typical of warm and dry conditions) arthropod fauna and that several specialist species, including most of the above-mentioned typical arthropods, had been completely lost from the Dutch calcareous grasslands (Aukema 1983; Cobben and Rozeboom 1983; de Boer 1983; Heijerman and Booi 1983; Mabelis 1983; Turin 1983; Van der Made 1983; Van Etten and Roos 1984; Koomen 1986).

Management was reinstated in most remaining sites around 1980 and consisted of shrub removal followed by mowing and/or grazing with a local sheep breed (*Mergelland schaap*) (Hillegers 1993; Willems 2001). This yielded a reduction in the dominance of the grass *Brachypodium pinnatum*, an improvement in vegetation structure and an improvement in plant species richness (Bobbink and Willems 2001). However, full restoration of plant communities was not accomplished (Bobbink and Willems 2001; Smits 2010). The effects on arthropod communities remained largely unknown (Bobbink and Willems 2001), but at least butterfly richness and abundance did not increase following this restoration management (WallisDeVries et al. 2002).

Aims and research questions

In this thesis I aim to increase our understanding at three distinct levels. Firstly, I aim to develop tools that provide mechanistic understanding of species-environment relationships, by investigating how to incorporate interactions in trait analyses. Secondly, I aim to increase our general understanding of species-environment relationships by investigating the ecological consequences of traits and trait interactions. Thirdly, I aim to provide applied conservation advice for the specific system I have studied.

The starting point for this thesis was formed by a number of applied projects (Smits et al. 2009; Van Noordwijk et al. 2012, 2013) that were part of the ‘Development and Management of Nature Quality’ (O+BN) program, commissioned by the Dutch Ministry of Economic affairs. In line with these projects I aim to unravel the main bottlenecks (i.e. the main problems preventing recovery) for arthropods in Dutch calcareous grasslands and to provide applied management advice to counter these. My research questions can be summarized as:

- 1) To what extent have arthropod communities in Dutch calcareous grasslands been restored over the past two decades of conservation management?
- 2) How can species’ traits and their interactions be used to gain insight in the mechanisms underlying species-environment relationships?
- 3) How are arthropods in calcareous grasslands affected by environmental stressors, in particular isolation, fragmentation, vegetation structure, microclimate and disturbance caused by grassland management?
- 4) Which strategies are most effective to restore and conserve arthropod communities in Dutch calcareous grasslands?

Thesis outline

This thesis consists of six research papers which provide answers to one or more of the research questions (Table 1). As arthropods form a large and heterogeneous species group, which is difficult to study in its totality, different selections of species are covered in each chapter (see Figure 4).

Chapters two and three describe observed species patterns and deal with the question what these patterns can tell us about the underlying mechanisms. In **chapter 2** I studied the changes in diversity patterns over 17 years of conservation management both in terms of species richness within sites and with respect to community similarity between sites. I studied seven different arthropod groups and vascular plants to get an impression of the differences in response to management between taxonomic groups. In **chapter 3** I developed life-history strategies for ants from literature. I used these to predict to which environmental conditions each species would be most vulnerable and applied them to field data.

Table 1. Research questions (see text) addressed in each thesis chapter.

Chapter	1) Arthropod communities restored?	2) Develop methodology	3) Species-environment theory	4) Management application
2) Biotic homogenization	X	X		
3) Ant strategies	X	X	X	X
4) Grazing review			X	X
5) Grazing experiment			X	X
6) Dispersal model		X	X	X
7) Site size & carabids		X	X	X

In chapters four and five I focussed on the impact of grazing management on arthropods. **Chapter 4** gives an extensive literature review of the patterns and processes of grassland arthropod responses to large herbivores. This yields a general framework that 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. **Chapter 5** describes a field study in which a single aspect of grazing impact on arthropods is studied in detail. Using the butterfly species Glanville fritillary (*Melitaea cinxia*), I studied how winter grazing affects caterpillar survival in the field.

Chapters six and seven focus on the landscape perspective. In **chapter 6** a computer model simulation was used to establish how dispersal traits, demographic vital rates and landscape characteristics interact and facilitate or inhibit dispersal in fragmented landscapes. The response of different species groups to a number of restoration strategies is modelled to establish whether conservation priorities differ between species. **Chapter 7** investigates how species-area relationships depend on habitat affinity, trophic level and dispersal ability in carabid beetles.

The final chapter (**chapter 8**) synthesizes the results from the previous chapters to answer the research questions formulated above. Specifically, I discuss: 1) what progress has been made with respect to the use of traits and their interactions in gaining mechanistic understanding of species-environment relationships; 2) new insights on the effects of various stressors on arthropod communities; 3) the main bottlenecks found for arthropod conservation in (Dutch) calcareous grasslands and their implications for management practice.

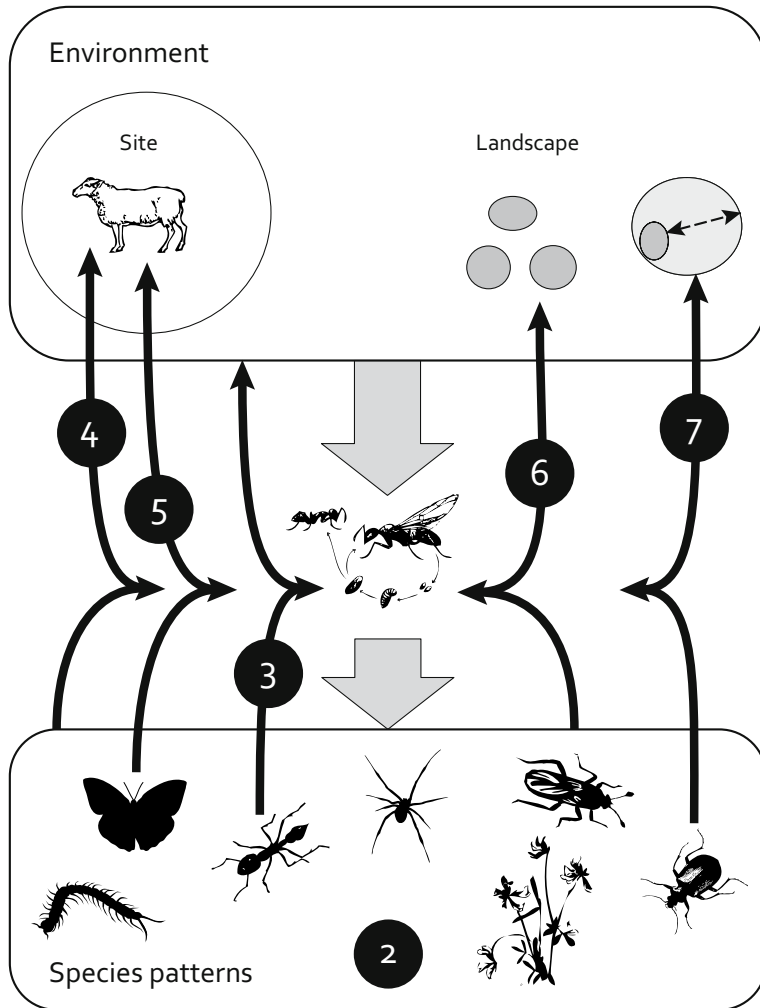


Figure 4. Representation of the thesis outline. Chapter 2 explores diversity patterns, while all other chapters investigate species-environment relationships. The focus of each chapter is depicted with respect to the taxonomic scope (broad in chapters 2, 4 & 6 and specific in chapters 3 (ants), 5 (a butterfly species) & 7 (carabid beetles)) and environmental factors addressed (none specifically in chapter 2, broad in chapter 3 and specific in chapters 4 (grazing), 5 (grazing), 6 (habitat fragmentation) & 7 (habitat area)).



Emptying pitfall traps during autumn grazing (Photo: Toos van Noordwijk)

Chapter 2

Biotic homogenization and differentiation in response to grassland management

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Abstract

Increased biotic homogenization is threatening genetic, taxonomic and functional diversity. Conservation management may be able to counteract biotic homogenization, as it aims to restore and maintain valuable habitats to support threatened species. We evaluate the usefulness of conservation management as a tool to counter biotic homogenization, by analysing shifts in diversity patterns over 17 years of calcareous grassland management for plants and a range of arthropod groups, covering four trophic levels. Changes in occurrence were analysed at the species level, which gave insight in which species contribute to homogenization or differentiation. Responses were compared between species differing in habitat affinity, dispersal ability, food specialisation and trophic level.

Diversity shifts over time differed markedly between taxonomic groups, irrespective of trophic level. Carabid beetles and weevils declined in species richness, while true bugs and millipedes increased. All groups showed considerable species-turnover. Overall biotic homogenization was recorded for carabid beetles, while compositional variation among sites increased for millipedes (differentiation). Habitat affinity, dispersal ability and food specialisation explained some of the variation in diversity shifts within groups, but results were not consistent across taxonomic groups and the explanatory power was generally low.

We conclude that conservation management can be a tool to counteract biotic homogenization, but only under specific circumstances. We observed both biotic homogenization and differentiation within our study sites, which holds important implications for future biotic homogenization studies. Thorough understanding of the underlying mechanisms is essential. Evaluating species-level patterns and incorporating species' traits are important steps towards unravelling these mechanisms.

Keywords

Beta-diversity; biodiversity; insects; nature conservation; species composition; trait.

Introduction

Biotic homogenization is non-random loss and gain of species that leads to reduced compositional variation among communities, usually caused by a loss of rare specialist species and an increase in common generalist species (McKinney and Lockwood 1999; Olden et al. 2004). The resulting genetic, taxonomic and functional impoverishment is viewed as a major threat to biodiversity (Olden et al. 2004; Mouillot et al. 2013). Biotic homogenization has recently been demonstrated to occur across nearly all taxonomic groups, spatial scales and grain sizes (Baiser et al. 2012), although remarkably few studies have simultaneously investigated changes in diversity patterns for more than one taxonomic group (Baiser et al. 2012, but see Shaw et al. 2010). At regional and local scales, homogenization is mainly caused by land-use change and habitat fragmentation, through a loss of specialist species and increased opportunities for (invasive) generalists (McKinney and Lockwood 1999; McKinney and Lockwood 2001).

The negative effects of local drivers of homogenization in semi-natural habitats can successfully be countered by particular restoration and conservation management, however, the relationship between management and biodiversity patterns remains complex. Conservation and restoration management can have multiple effects on diversity patterns (Figure 1). Management is usually considered successful if it restores and maintains valuable habitats to support threatened species, which can lead to a higher local diversity and a larger regional species pool (Bobbink and Willems 1993; Hobbs and Norton 1996; Pöyry et al. 2004). Ideally, such restoration also increases the compositional variation among sites, with management strengthening inherent environmental differences between sites. However, if all sites improve in the same way compositional variation among sites will decrease. Management can also fail to deliver increased local and regional diversity, e.g. if characteristic species are unable to return due to dispersal limitations (Donath et al. 2003; Ozinga et al. 2005; Woodcock et al. 2010) or because management leads to decreased site-to-site habitat variation due to homogenised management actions (Konvicka et al. 2008; Verberk et al. 2010a). Conservation management may thus have contrasting effects on diversity patterns, leading to increased biotic differentiation or conversely, amplifying biotic homogenization. These patterns may also differ between species groups, even within the same sites.

Different species and taxonomic groups have repeatedly been shown to differ in their response to landscape structure (Dormann et al. 2007) and conservation management (Kruess and Tscharntke 2002b; Oertli et al. 2005; chapter 4). While species with a well-developed dispersal ability colonise restored habitat at a higher rate (Ozinga et al. 2005; Lambeets et al. 2009; Öckinger et al. 2010; Woodcock et al. 2010; Woodcock et al. 2012), characteristic species and food specialists show a poorer dispersal capacity (Bonte et al. 2003; Woodcock et al. 2012) and are generally more vulnerable to habitat degradation (Römermann et al. 2008; Öckinger et al. 2010). In general however, they are expected to respond more positively to prolonged management than non-characteristic and food generalist species, as habitat conditions improve most for them. In addition, a species' trophic position modulates its sensitivity to processes operating at larger spatial scales (Holt et al. 1999; Vanbergen et al. 2010), making higher trophic levels more vulnerable to habitat fragmentation (Purtauf et al. 2005; Krauss et al. 2010).

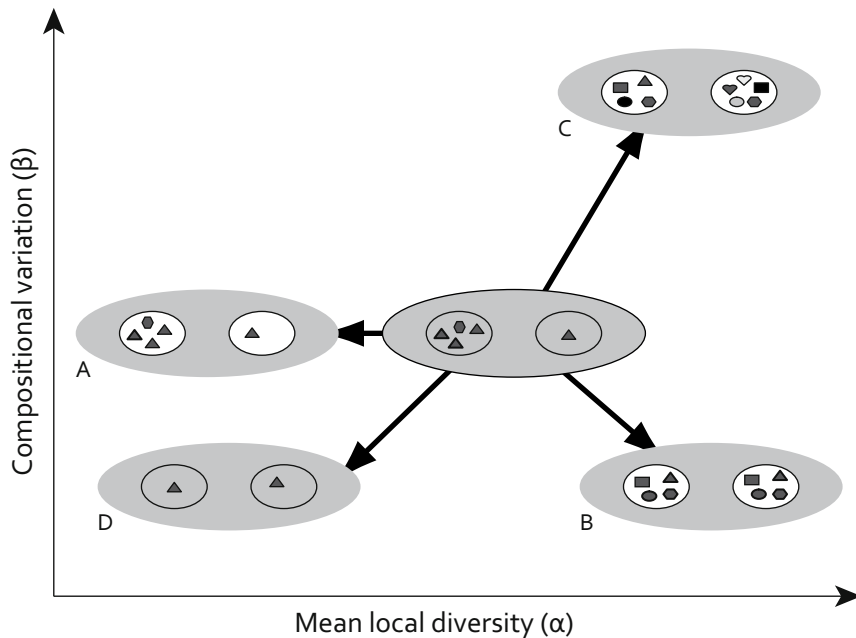


Figure 1. Potential effects of conservation management on local diversity and the compositional variation among sites (β -diversity). Each situation (A-D) depicts two hypothetical sites (small circles with symbols) within a region. The grey area depicts the presence of common generalist species, symbols and colors depict different specialist species which the conservation management aims to increase. From the initial situation (in the middle), management can cause A) decreased presence of generalist species, but no increase in specialists e.g. due to dispersal limitations; B) decreased presence of generalists and an increase in specialists, but identical composition in all sites; C) decreased presence of generalists and an increase in specialists, restoring the unique character of each site, causing increased compositional variation; D) yet another disturbance leading to a further decrease in characteristic species (failure to deliver increased habitat suitability).

In this study we applied a species-based approach to investigate to what degree restoration actions induce shifts in diversity patterns. Our study was carried out in Dutch calcareous grasslands, which were resurveyed after 17 years of management. Calcareous grasslands have suffered from agricultural intensification, eutrophication and abandonment of traditional farming practices (Baldock et al. 1996; Ostermann 1998; Balmer and Erhardt 2000), which resulted in a strong decline in species richness, especially among initially rare, characteristic plant and arthropod species (WallisDeVries et al. 2002; Smits 2010), which in turn led to biotic homogenization (Polus et al. 2007; Smits 2010; Ekroos et al. 2010). Restoration and conservation management have been reinstated to mitigate these negative effects of land-use change and eutrophication and are expected to counteract biotic homogenization. To test the generality of diversity responses we studied a wide range of taxonomic groups and tested whether the species-specific responses were related to relevant ecological traits like dispersal ability, trophic level and the degree of food specialisation of species.

Methods

Study region

The study was conducted in eight calcareous grasslands in South-Limburg, the Netherlands (see Appendix 1 and chapter 3 for an extensive site description). All sites were originally grazed by sheep until the early 20th century and were subsequently abandoned or irregularly managed for several decades. Despite some spatiotemporal variation in management intensity, the conservation management resulted in a similar short vegetation sward in all managed sites (Willems 2001).

Data collection

Arthropods were sampled by means of standardised pitfall sampling in 1988, shortly after or around the time of renewed structural management and again in 2005 or 2006 (referred to as 2005). All true bugs (Heteroptera), carabid beetles (Coleoptera, Carabidae), weevils (Coleoptera, Curculionidae), ants (Hymenoptera, Formicidae), spiders (Araneida), woodlice (Isopoda) and millipedes (Diplopoda) were identified to species level (see Appendix 2 for more details, including nomenclature). Because of the applied pitfall sampling, our data represent the ground dwelling proportion of the sampled species groups, rather than a complete overview of species. Vegetation data were taken from the Dutch Vegetation Database (Schaminée et al. 2012) covering the periods 1970-1992 (referred to as 1988) and 1997-2007 (referred to as 2005). Because sampling effort differed between the two sampling periods, we randomly subsampled the relevés for each site and period to obtain a balanced dataset (see Appendix 2 for more details).

We collected ecological traits from literature on the trophic level (primary producers, first order consumers, predators and detritivores), habitat affinity (characteristic versus non characteristic species for calcareous grasslands), food specialisation (monophagous, oligophagous and generalist) and dispersal ability (see Appendix 3 for traits and literature sources). Species which shift in trophic level during their life-cycle (notably a few carabid species) were classified according to their larval characteristics, as larvae are generally less mobile and more vulnerable to adverse microclimatic conditions and food shortages than adults (Thiele 1977; Bourn and Thomas 2002; Fartmann and Hermann 2006; chapter 7). Good and poor dispersal ability were defined respectively as presence or absence of long distance dispersal strategies (LDD) in plants and as presence or absence of individuals capable of active flight for carabid beetles, weevils and true bugs. For ants dispersal ability was judged from their life history strategy (chapter 3), with species mainly founding new nests through social-parasitism or nest-splitting defined as poor dispersers. For millipedes and woodlice body size was used as a substitute for dispersal ability. For spiders dispersal ability was categorized based on behaviour traits including ballooning. For all taxonomic groups a third category was made, containing species for which the dispersal ability is intermediate or uncertain.

Statistical analysis

All statistical analyses were performed per taxonomic group. For vascular plants all analyses were performed for each of the replicate datasets and results were averaged. First, the mean species richness per site and sampling period was calculated (α -diversity) as well as the total number of species for each sampling period (γ -diversity). Changes in α -diversity per site were calculated using the formula:

$$\Delta\alpha = \frac{\alpha[\text{new}] - \alpha[\text{old}]}{\alpha[\text{new}] + \alpha[\text{old}]}$$

This means that $\Delta\alpha$ can range from -1 to 1 and that negative values represent a decrease in species richness, while positive values represent an increase. Changes in γ -diversity were calculated analogously. Generalized estimation equations were used to test for significant changes in α -diversity (dependent variable) over time (independent variable), using a Poisson distribution and sites as the grouping variable. Next, to visualise species-turnover rates, the fraction of occupied sites in 1988 was plotted against the fraction of occupied sites in 2005 for each species. The compositional variation among sites (β -diversity) was quantified with a model-based multiple-site metric D developed by Baeten et al. (2014). The metric is derived from a species-level measure of heterogeneity of occurrence (D_i), summed across the species. It is low if the community data set has many species that are either rare (absent in most sites) or prevalent (present in most sites) (low D_i values), i.e., such species do not contribute much to the compositional variation among communities. Homogenization occurs if many species decrease their heterogeneity of occurrence over time ($\Delta D_i < 0$, so their sum $\Delta D < 0$), i.e., rare species that became rarer or prevalent species that became more prevalent. Differentiation similarly occurs when most species increase their heterogeneity ($\Delta D_i > 0$). The significance of species-level and community-level homogenization or differentiation is tested with a permutation test (999 permutations). Finally, we tested for effects of the traits trophic level, dispersal ability, habitat affinity and food specialism (independent variables) on the individual species responses ΔD_i and change in occupancy over time (fraction occupied sites 1988 minus fraction occupied sites 2005) using permutational analysis of variance (PERMANOVA, 999 permutations). Only main traits and two-way interactions were included and preliminary tests were performed to determine the order of traits to be added to the model (most influential traits were added first). All analyses were carried out in R (R Development Core Team 2013) using the packages Geepack (Højsgaard et al. 2006) and Vegan (Oksanen et al. 2013).

Results

Changes in alpha- and gamma diversity over time differed between taxonomic groups with no consistent patterns for groups belonging to the same trophic level (Figure 2, Table 1). Carabid beetles decreased in alpha- and gamma diversity, while true bugs and millipedes showed an increase in both alpha and gamma diversity. For weevils alpha diversity decreased over time, but gamma diversity stayed constant. All other groups showed only minor changes in alpha and gamma diversity. Few species had similar relative frequencies in both sampling periods (along diagonal in Figure 3), implying considerable species turn-over over time for all groups. Nevertheless, for only two groups the compositional

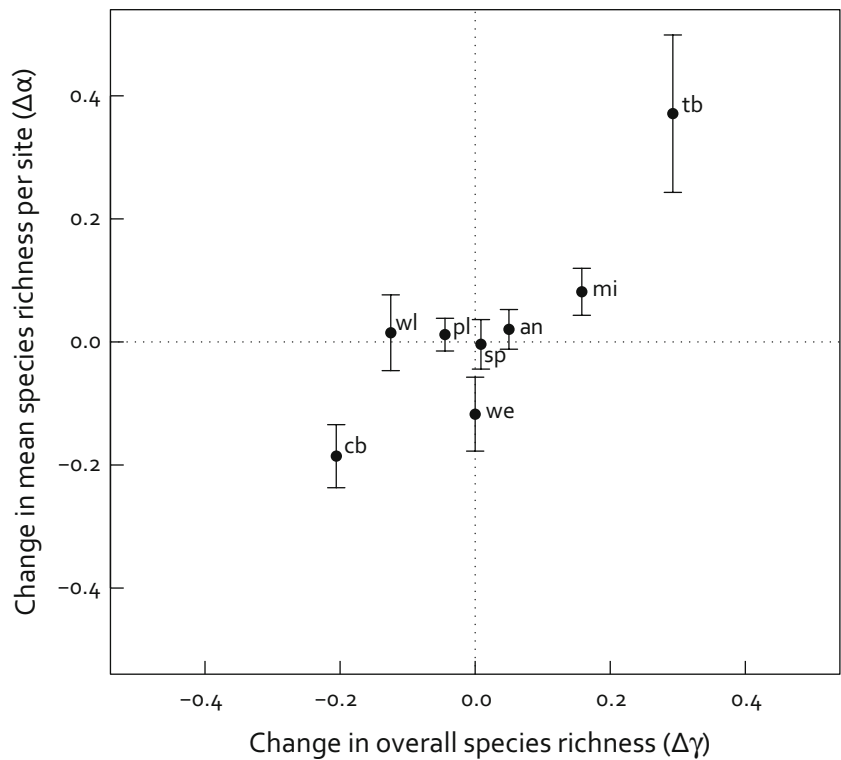


Figure 2. Change in mean species richness per site between 1988 and 2005 (± 1.0 SE) against the change in overall species richness over the same period per taxonomic group (an = ants, cb = carabid beetles, mi = millipedes, pl = vascular plants, sp = spiders, tb = true bugs, we = weevils, wl = woodlice). Positive changes indicate an increase in richness, negative values represent a decrease.

Table 1. Change in mean species richness per site between 1988 and 2005 ($\Delta \alpha$ -diversity), p-value for the generalized estimation equation (GEE) testing for significant changes in α -diversity and change in overall species richness ($\Delta \gamma$ -diversity) per taxonomic group. Groups showing a significant change in α -diversity ($p < 0.05$) are bold.

Trophic level	Taxonomic group	$\Delta \alpha$ -diversity	p-value	$\Delta \gamma$ -diversity
Primary producers	Plants	0.012	0.588	-0.045
Detritivores	Woodlice	0.015	0.785	-0.125
	Millipedes	0.081	0.025	0.157
1 st order consumers	True bugs	0.371	0.008	0.293
	Weevils	-0.117	0.011	0.000
Predators	Carabid beetles	-0.186	<0.001	-0.206
	Spiders	-0.004	0.922	0.009
	Ants	0.020	0.508	0.050

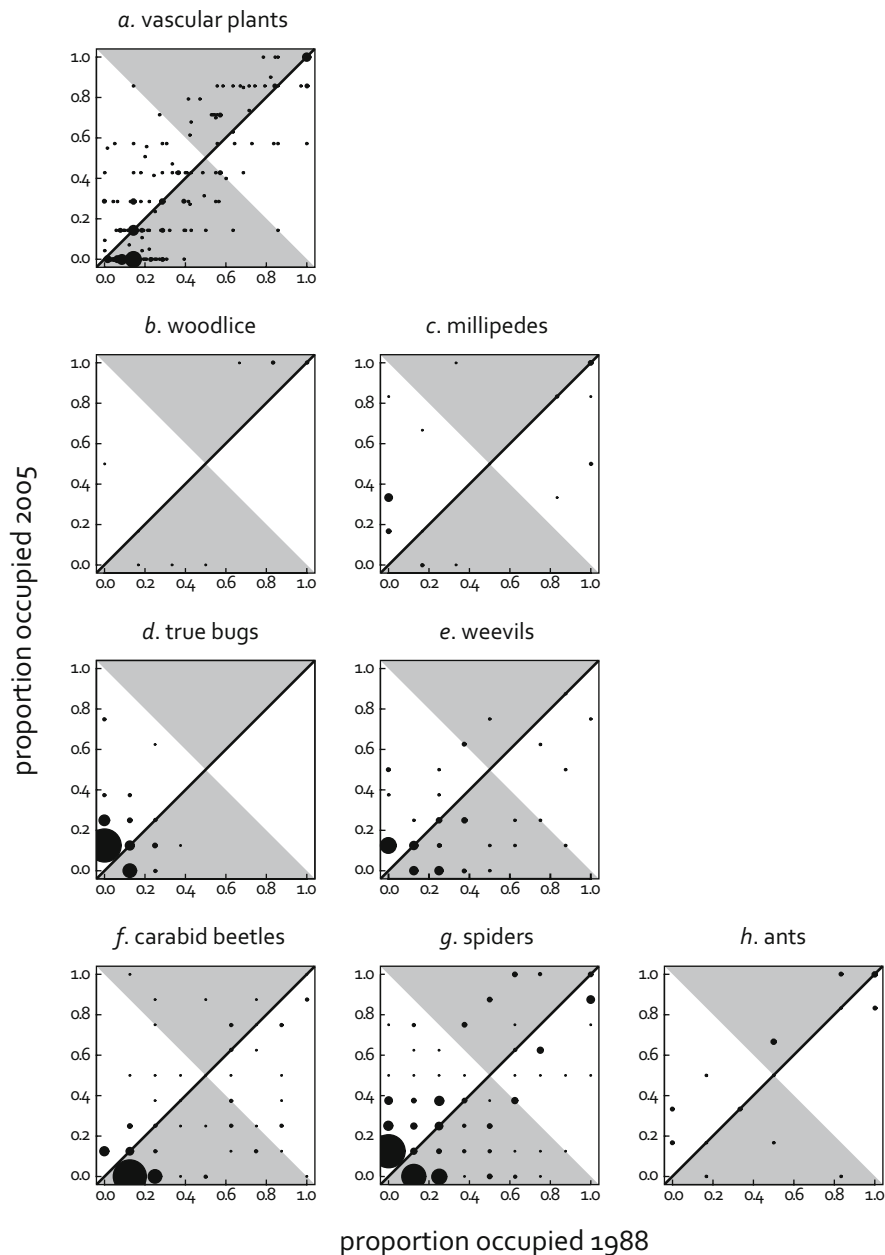


Figure 3. Proportion of occupied sites in 2005 versus 1988 for each species per taxonomic group ordered by overall trophic level. Overlapping species are represented as larger circles. The diagonal line represents no change in the proportion of occupied sites between the sampling periods. The area below this line represents a decrease in occurrence, the area above represents an increase. Species with frequency changes that fall in the upper and lower triangles (grey) cause biotic homogenization (rare becoming rarer or prevalent becoming more prevalent), species in the white triangles cause increased differentiation.

Table 2. Results of the delta deviance analyses per taxonomic group. Significant results ($p < 0.05$) are given in bold and represent overall biotic homogenization for negative values of delta deviance and overall differentiation for positive values of delta deviance.

Trophic level	Taxonomic group	n sites	n species	ΔD	p
Primary producers	Plants	7	223	-97.51	0.447
Detritivores	Woodlice	6	10	-31.50	0.119
	Millipedes	6	25	60.23	0.030
1st order consumers	True bugs	8	64	183.69	0.061
	Weevils	8	54	-16.04	0.625
Predators	Carabid beetles	8	91	-199.89	0.029
	Spiders	8	151	1.309	0.988
	Ants	6	23	13.24	0.612

changes caused the compositional variation among sites to change as well (Figure 3). For millipedes, significant differentiation of the study sites was observed (Table 2), while there was a trend towards differentiation for true bugs ($p = 0.06$). Carabid beetle communities homogenized, mainly because many initially rare species became rarer over time (Figure 3, Table 2).

Habitat affinity was significantly related to the decrease or increase of spiders (Permanova: $df = 1, 144$; $R^2 = 0.036$; $p = 0.026$), with characteristic species increasing more than others (Figure 4a). No single effect of habitat affinity was found for the other taxonomic groups (Appendix 4). The interaction between habitat affinity and dispersal ability significantly explained which spider species contributed to overall homogenization or differentiation (Permanova: $df = 1, 144$; $R^2 = 0.044$; $p = 0.011$). Good dispersers initially occurred in more sites than poor dispersers. For the initially rare characteristic species with poor dispersal ability an increase in occurrence led to an increase in compositional variation. For the initially more widespread characteristic species with good dispersal ability the same increase in occupancy had no effect on the compositional variation between sites. Conversely, the decline of non-characteristic species with poor dispersal ability led to homogenization, as initially rare species became rarer. The same decline had no effect on the compositional variation among sites for non-characteristic species with good dispersal abilities, which were initially more widespread (Figure 4a). For plants there was a trend towards an interaction (Permanova: $df = 1, 219$; $R^2 = 0.018$; $p = 0.060$) between habitat affinity and dispersal ability on the decrease or increase in occurrence (Figure 4b), with characteristic species increasing more than other species, but only if they exhibit long distance dispersal strategies. Poorly dispersing characteristic species tended to decrease in occurrence, even more so than non-characteristic species. For woodlice, body size, which was taken as a proxy for dispersal ability, had a significant effect on the change in occurrence over time (Permanova: $df = 1, 6$; $R^2 = 0.70$; $p = 0.003$). Large woodlice increased in occurrence, while small woodlice decreased over time (Figure 4c).

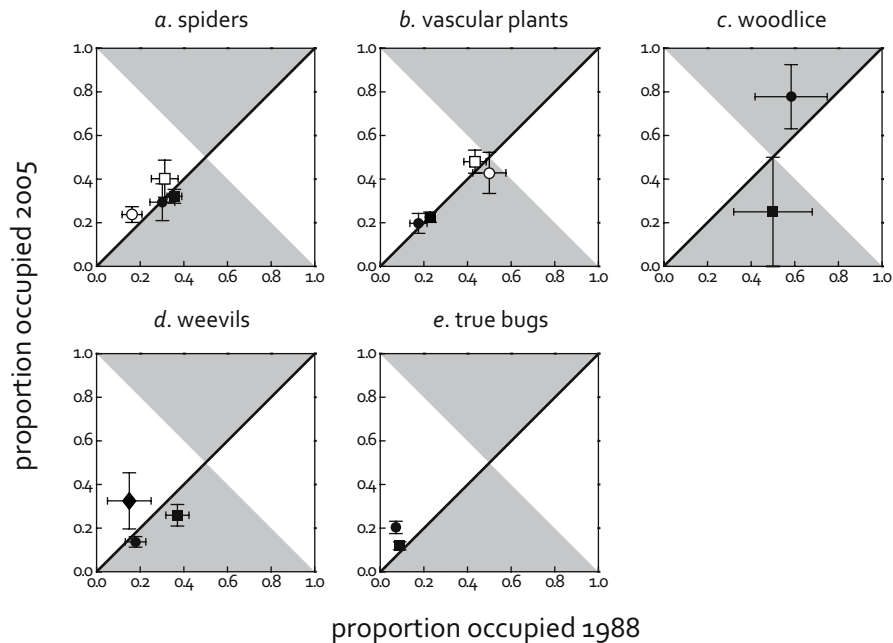


Figure 4. Mean proportion of occupied sites in 2005 versus 1988 (± 1.0 SE) for species from different trait categories, with white symbols depicting habitat specialists and black symbols depicting habitat generalist. Only the five taxonomic groups showing (near) significant trait effects are shown. a. Spiders classified as habitat specialists and habitat generalists with good (squares) and poor (circles) dispersal ability. b. Vascular plants classified as habitat specialists and habitat generalists with good (squares) and poor (circles) dispersal ability. c. Woodlice larger (circle) and smaller (square) than 10.5 mm in body size. d. Weevils classified as polyphagous (square), oligophagous (circle) and monophagous (diamond). e. true bugs classified as herbivorous (circle) and carnivorous (square). The diagonal line represents no change in the proportion of occupied sites between the sampling periods. The area below this line represent a decrease in occurrence, the area above represents an increase. The upper and lower triangles (grey) are associated with biotic homogenization, the left and right triangles (white) are associated with increased differentiation between sites.

For weevils, a significant difference in occurrence change was found for species differing in their degree of food type specialization (Permanova: $df = 1, 47$; $R^2 = 0.089$; $p = 0.024$). Monophagous species on average increased in occurrence, while oligophagous and polyphagous species tended to decrease in occurrence over time (Figure 4d). With respect to trophic level, no significant effects were found within taxonomic groups, although for true bugs there was a near significant effect (Permanova: $df = 1, 50$; $R^2 = 0.062$; $p = 0.057$), with phytophagous species increasing more than zoophagous species (Figure 4e).

Discussion

Conservation management has been suggested to be an effective tool to counteract diversity loss at regional and local scales (Doxa et al. 2012). However, our results demonstrate that biotic differentiation and biotic homogenization can both occur over a 17 year-period of calcareous grassland management, depending on the species' taxonomical and functional classification.

We found increased local species richness and community differentiation in millipedes and true bugs, while carabid beetle species richness decreased, leading to biotic homogenization. For weevils, the decline of local species richness was not associated with changes in compositional variation among sites. The observed changes in compositional variation were not caused by replacement of characteristic species by non-characteristic species or vice-versa. Rather, they were paralleled by an overall increase or decrease in species richness, which is in line with the results of other meta-analysis (Baeten et al. 2014; Baiser et al. 2012). In contrast to the taxonomic groups that exhibited overall homogenization or differentiation we did observe replacement of non-characteristic species by characteristic species for spiders without any changes in overall compositional variation. This implies a process of replacement independent of the initial occurrence, because indeed, if both rare and prevalent characteristic species increase over time, there is no net-effect on the compositional variation. These differential responses across taxa are in accordance with the few reports so far (Devin et al. 2005; Shaw et al. 2010). The reason for this variation in responses between taxonomic groups is that many different factors, including land-use change, climate change, increased nitrogen levels, biotic exchange and vegetation structure affect species distributions (Morris 2000; Sala 2000) and the relative importance of these factors differs among taxonomic groups (Dormann et al. 2007; chapter 4). Taxonomic groups also differ in their response to conservation management such as grazing itself (chapter 4).

In addition to the variation in responses between taxonomic groups, species within each group also differ in life-history, and hence in vulnerability to all the different factors affecting biodiversity (Stearns 1976; Southwood 1977). This causes a multitude of responses within each group, which are likely to cancel each other out and obscure overall patterns. The use of traits may help to disentangle contrasting effects. For weevils we found an effect of food type specialization with food specialists responding more positively than food generalists. This implies that conditions generally increased for these food specialists, which all feed on forbs that are well adapted to dry, nutrient poor conditions. Analysis of the trait-responses within each taxonomic group also revealed some evidence, albeit weak, for dispersal barriers limiting (re-) colonization of restored sites. Such dispersal barriers, caused by fragmentation and site isolation, were previously reported for these sites in a study on ants (chapter 3). For woodlice we found a strong correlation between occurrence change and body size, which was used as a proxy for dispersal ability. While large bodied species (>10 mm) increased in occurrence, small-bodied species declined. Nonetheless, no hard conclusions can be drawn from this relationship as body size is equally related to other responses including drought resistance. Small species are more vulnerable to drought than larger species (Dias et al. 2012), presenting an alternative explanation for the observed relationship. For vascular plants, we found a near significant interaction

between habitat affinity and dispersal ability: characteristic species increased only if they also have long-distance dispersal mechanisms. This indicates that site conditions may have improved but that characteristic species with poor dispersal ability may be unable to recolonize the sites (Ozinga et al. 2005; Smits 2010). We need, however, to point-out that although these traits give some insight in the mechanisms causing observed diversity changes, the explanatory power of single traits in our study was generally low. This is at least partly due to the presence of interactions among traits and the general contingency of trait value on a species' body-plan and environment (Verberk et al. 2013). This may explain why no effect of trophic level was found even though this trait has frequently been demonstrated to alter species-environment relationships (Van Nouhuys 2005; Vanbergen et al. 2010).

Our results suggest that the conservation management in the Dutch calcareous grasslands has generally benefitted true bugs, millipedes and characteristic spider species, while it may have had adverse effects on carabid beetles and weevils (but not food specialists). It seems that some barriers impeding further improvement remain, including potential dispersal limitations. However, it is difficult to disentangle the exact effects of conservation management from other factors that have affected the study sites simultaneously, such as changes in the wider landscape and natural population fluctuations. Especially carabid beetles are known to exhibit considerable annual population fluctuations (Baars and Van Dijk 1984; Den Boer 1985, 1990a; Brooks et al. 2012), which can be synchronized over large area's (Baars and Van Dijk 1984; Östman 2005) and are for a large part triggered by weather conditions (Baars and Van Dijk 1984; Hengeveld 1985). Such population fluctuations may explain part of the observed pattern for carabid beetles, but the changes in vegetation structure, biomass, microclimate and disturbance regime caused by the conservation management are so large (Willems 2001; chapter 3) that it is unlikely that conservation management has not contributed to the observed patterns. Altogether, our results highlight the necessity to adopt a wide taxonomic scope when studying biodiversity patterns, especially if the aim is to evaluate or design strategies to tackle diversity loss.

Implications

Our study demonstrates that conservation management can contribute to biotic differentiation (as shown for the millipedes) and hence can be a tool to counteract biotic homogenization at local and regional scales. However, we also demonstrate that successful management (in terms of increased occurrence of characteristic species) does not always lead to increased compositional variation among sites (e.g. the spiders in our study). Theoretically, successful conservation management can even contribute to biotic homogenization in a positive way, e.g. if it causes characteristic species to be present in all study sites. Therefore, biotic homogenization should not by definition be considered as a process that needs to be avoided and countered. This underlines the importance of looking beyond diversity patterns and gaining insight in the mechanisms driving them. The large number of factors affecting diversity patterns, especially in semi-natural habitats undergoing restoration or renewed conservation management, cause a multitude of responses both within and between taxonomic groups. Identification of the most influential factors, both within individual sites and in the wider landscape

(e.g. fragmentation, isolation and pollution) is essential to develop effective strategies to halt the loss of biodiversity across taxonomic groups. Evaluating species-level patterns and incorporating species' traits are important steps towards this goal.

Acknowledgements

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Appendix 1. Additional information about the study sites

The sites range in surface area from one to five hectares. One site (Wrakelberg) was partly used as arable land for a short period in the 1960s, before being converted back to calcareous grassland. Renewed regular management was introduced in all sites between 1978 and 1990 and consists of sheep grazing, mowing or a combination of these, conducted at least once a year (Willems 2001). In sites suffering severe grass- or scrub encroachment the conservation management phase was preceded by a restoration phase with relatively intensive sheep grazing and scrub clearance.

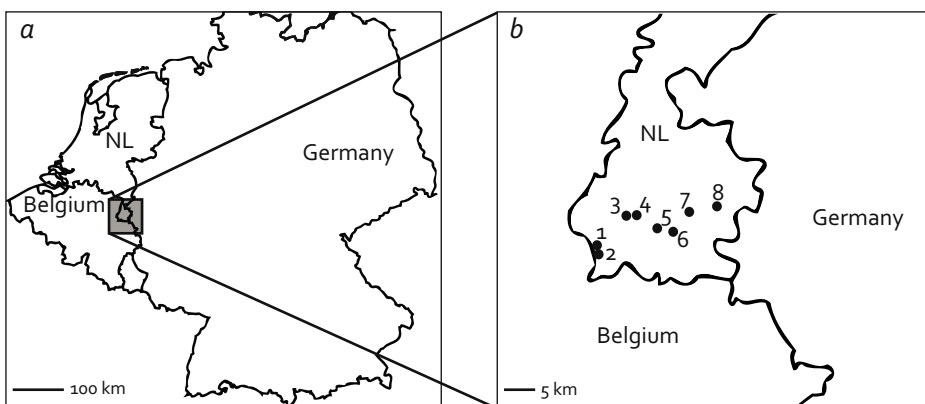


Figure A1. Location of the sites a) in NW-Europe and b) within Zuid-Limburg in the Netherlands ($50^{\circ} 51' N$, $5^{\circ} 52' E$, altitude 50–150 m above sea level). The numbers refer to the sites: 1. Sint Pietersberg Cannerhei (SPCa); 2. Sint Pietersberg Poppelmondedal (SPPo); 3. Bemelen Strohberg (BemS); 4. Bemelen Winkelberg (BemW); 5. Laamhei (Laam); 6. Berghofweide (Bhof); 7. Wrakelberg (Wrak); 8. Kunderberg (Kund).

Appendix 2. Field sampling methods

Arthropod sampling

Arthropod sampling was conducted using a series of pitfall traps (8.5 cm diameter, approximately 5 meters apart). Each pitfall trap was covered with a 10 cm by 10 cm plate placed at a height of about 2 cm above the ground. Traps were filled with 0.1-0.2 L of formaldehyde solution (5%) to which a few drops of liquid soap were added, to reduce surface tension. Each site contained several pitfall trap series, placed at least 25 meters (but mostly more) apart. The number of series differed between sampling periods and sites with a minimum of two series per site. To obtain equal sampling efforts across sites and periods we randomly selected two series per site that were used during both sampling periods for our analysis.

Traps operated from April to October and were serviced every three weeks. For some taxonomic groups a more restricted sampling period was used, but in all cases sampling periods per group were matched for the two sampling years. For the ants we used all data collected from May to September 2005 and all data from April to August 1988, resulting in a trapping period of 135-140 days for each period. Two sites (SPCa and SPPo) were excluded from this analysis as they were not sampled in 1988. For the spiders, data were used covering the period from early April to mid August, omitting additional sampling periods from the 2005 data to match the sampling periods available for 1988. Only true spiders (Arachnidae) were included in the analysis. For woodlice and millipedes data were only available per site for 1988 (Mabelis and Verboom 2009), and not for each separate pitfall trap series. Therefore, extra pitfall trap series were selected for most sites for the 2005 data to match the 1988 sampling campaign as closely as possible. Sites SPCa and SPPo were viewed as one site in 1988 and were therefore taken together in the analysis for these two groups. Similarly sites BemW and BemS were analysed as a single site.

Vascular plant sampling

The number of available relevees per site and period ranged from 5 to 91, with individual relevee sizes ranging from one to nine square metres. In general relevee sizes were similar within sites across time periods. Moreover, sites and periods with few available relevees tended to have data collected for larger surface areas. To generate comparable sampling efforts across both time periods, random subsamples of the relevees for each site and period were taken. This was repeated twenty times to create twenty permutation datasets. The number of relevees used per site was identical for both time periods and was equal to the number of available relevees for the least sampled period, with a maximum of twenty relevees. This threshold of twenty relevees was chosen based on visual inspection of species accumulation curves for all sites. For one site (BemS) there were no historic relevees available and this site was excluded from the vascular plant analysis.

Nomenclature and taxonomy

Nomenclature followed Van der Meijden (2005) for vascular plants, Turin (2000) for carabid beetles, Berg and Wijnhoven (1997) for woodlice, Blower (1985) for millipedes, Noordam (1998) for spiders, Aukema and Rieger (1995-1999) for true bugs, Heijerman (1993) for weevils and Boer (2010) for ants. Where changes in taxonomy have occurred (lumping or splitting of species) between 1988 and 2006, we grouped species as long as they shared the same traits. This was done for the ants *Formica clara* and *F. rufibarbis*, *Tetramorium impurum* and *T. caespitum*, and *Tapinoma erraticum* and *T. subboreale*. For a number of vascular plants identifications were ambiguous across time periods or were not always identified to species level. Therefore we grouped: *Acer* species, *Festuca filiformis* and *F. ovina*, *Rhamnus* species, *Rosa* species and *Rubus* species.

Appendix 3. Trait data

Table A1. Literature used for each taxonomic group to compile the list of traits and species attributes (trophic level, habitat affinity, food specialisation and dispersal ability).

Trophic level	Taxonomic group	References
Primary producers	Plants	Kleyer et al. 2008 Ozinga et al. 2009
Detritivores	Woodlice	M.P. Berg pers. obs. Berg and Wijnhoven 1997 Gruner 1966
	Millipedes	M.P. Berg pers. obs. Blower 1985
1 st order consumers	True bugs	Wachmann et al. 2004 Wachmann et al. 2005 Wachmann et al. 2007 Wachmann et al. 2008
	Weevils	Dieckmann 1980 Everts 1903 Morris 1997 Morris 2002 Rheinheimer and Hassler 2010 Scherf 1964
Predators	Carabid beetles	Saska 2004 Saska 2005 Turin 2000
	Spiders	Bell et al. 2005 Lambeets et al. 2008 D. Bonte pers. obs.
	Ants	Seifert 2007 Chapter 3

Table A2. Trait attributes for each species listed per taxonomic group. Only traits and attributes showing variation within the taxonomic group are given: trophic level (1 = primary producer; 2 = herbivore; 3 = detritivore; 4 = carnivore), habitat affinity (1 = dry grassland specialist; 0 = other), food specialisation (1 = polyphagous; 2 = oligophagous; 3 = monophagous) and dispersal ability (0 = poor dispersal ability, 1 = medium dispersal ability; 2 = good dispersal ability). Mean body size in mm is given as a proxy of dispersal ability for woodlice and millipedes.

Spiders	hab.spec	food.spec	disp	Spiders (continued)	hab.spec	food.spec	disp
<i>Achaearanea riparia</i>	0	1	1	<i>Clubiona diversa</i>	0	1	2
<i>Aculepeira ceropodia</i>	0	1	2	<i>Clubiona lutescens</i>	0	1	2
<i>Aelurillus v-insignitus</i>	1	1	0	<i>Clubiona neglecta</i>	0	1	2
<i>Agelena labyrinthica</i>	0	1	2	<i>Clubiona pallidula</i>	0	1	2
<i>Agroeca brunnea</i>	0	1	0	<i>Clubiona reclusa</i>	0	1	2
<i>Agroeca cuprea</i>	1	1	2	<i>Clubiona terrestris</i>	0	1	2
<i>Agroeca proxima</i>	0	1	2	<i>Cnephalocotes obscurus</i>	0	1	2
<i>Agyneta decora</i>	0	1	2	<i>Coelotes inermis</i>	0	1	0
<i>Alopecosa accentuata</i>	0	1	2	<i>Coelotes terrestris</i>	0	1	0
<i>Alopecosa barbipes</i>	1	1	0	<i>Dicymbium brevisetosum</i>	0	1	2
<i>Alopecosa cuneata</i>	1	1	2	<i>Dicymbium nigrum</i>	0	1	2
<i>Alopecosa fabrilis</i>	1	1	0	<i>Dicymbium tibiale</i>	0	1	2
<i>Alopecosa inquilina</i>	1	1	0	<i>Diplocephalus cristatus</i>	0	1	2
<i>Alopecosa pulverulenta</i>	0	1	2	<i>Diplocephalus latifrons</i>	0	1	2
<i>Alopecosa striatipes</i>	1	1	0	<i>Diplocephalus picinus</i>	0	1	2
<i>Apostenus fuscus</i>	0	1	1	<i>Diplostyla concolor</i>	0	1	2
<i>Araneus diadematus</i>	0	1	2	<i>Dipoena coracina</i>	0	1	0
<i>Araneus quadratus</i>	0	1	2	<i>Dismodicus bifrons</i>	0	1	0
<i>Arctosa figurata</i>	1	1	0	<i>Drassodes cupreus</i>	0	1	0
<i>Arctosa lutetiana</i>	1	1	0	<i>Drassodes lapidosus</i>	0	1	0
<i>Argenna subnigra</i>	1	1	2	<i>Drassodes pubescens</i>	0	1	0
<i>Argiope bruennichi</i>	0	1	2	<i>Dysdera erythrina</i>	0	2	0
<i>Atypus affinis</i>	1	1	2	<i>Enoplognatha latimana</i>	0	1	2
<i>Atypus piceus</i>	1	1	0	<i>Enoplognatha ovata</i>	0	1	2
<i>Aulonia albimana</i>	1	1	0	<i>Enoplognatha thoracica</i>	0	1	2
<i>Bathypantes gracilis</i>	0	1	2	<i>Eperigone trilobata</i>	0	1	2
<i>Bathypantes nigrinus</i>	0	1	2	<i>Episinus angulatus</i>	0	1	0
<i>Bathypantes parvulus</i>	0	1	2	<i>Erigone atra</i>	0	1	2
<i>Centromerita bicolor</i>	0	1	2	<i>Erigone dentipalpis</i>	0	1	2
<i>Centromerita concinna</i>	0	1	2	<i>Erigone longipalpis</i>	0	1	2
<i>Centromerus aequalis</i>	0	1	1	<i>Erigonella hiemalis</i>	0	1	0
<i>Centromerus capucinus</i>	0	1	1	<i>Ero cambridgei</i>	0	2	2
<i>Centromerus expertus</i>	0	1	1	<i>Ero furcata</i>	0	2	2
<i>Centromerus leruthi</i>	0	1	1	<i>Euophrys aequipes</i>	1	1	0
<i>Centromerus pabulator</i>	0	1	1	<i>Euophrys frontalis</i>	0	1	2
<i>Centromerus persimilis</i>	0	1	2	<i>Euryopsis flavomaculata</i>	0	2	2
<i>Centromerus prudens</i>	0	1	2	<i>Gonatium rubens</i>	0	1	2
<i>Centromerus sylvaticus</i>	0	1	2	<i>Gonyldiellum vivum</i>	0	1	2
<i>Ceratinella brevipes</i>	0	1	2	<i>Hahnina helveola</i>	0	1	0
<i>Ceratinella brevis</i>	0	1	2	<i>Hahnina montana</i>	0	1	2
<i>Ceratinella scabrosa</i>	0	1	2	<i>Hahnina nava</i>	0	1	2
<i>Ceratinopsis stativa</i>	1	1	0	<i>Hahnina pusilla</i>	0	1	2
<i>Cheiracanthium erraticum</i>	1	1	0	<i>Haplodrassus kulczynskii</i>	1	1	0
<i>Cheiracanthium virescens</i>	0	1	2	<i>Haplodrassus signifer</i>	1	1	0
<i>Cicurina cicur</i>	0	1	0	<i>Haplodrassus umbratilis</i>	1	1	0
<i>Clubiona compta</i>	0	1	2	<i>Harpacea hombergi</i>	0	1	0
<i>Clubiona corticalis</i>	0	1	2	<i>Heliophanus cupreus</i>	0	1	2

Table A2. continued

Spiders (continued)	hab.spec	food.spec	disp	Spiders (continued)	hab.spec	food.spec	disp
<i>Heliophanus flavipes</i>	0	1	2	<i>Pachygnatha clercki</i>	0	1	2
<i>Histopona torpida</i>	0	1	2	<i>Pachygnatha degeeri</i>	0	1	2
<i>Hypsosinga albovittata</i>	1	1	2	<i>Pachygnatha listeri</i>	0	1	2
<i>Jacksonella falconeri</i>	1	1	0	<i>Panamomops inconspicuus</i>	0	1	1
<i>Lepthyphantes ericaeus</i>	0	1	2	<i>Panamomops sulcifrons</i>	0	1	1
<i>Lepthyphantes flavipes</i>	0	1	2	<i>Pardosa agrestis</i>	0	1	2
<i>Lepthyphantes insignis</i>	0	1	2	<i>Pardosa agricola</i>	1	1	0
<i>Lepthyphantes mengei</i>	0	1	2	<i>Pardosa amentata</i>	0	1	2
<i>Lepthyphantes pallidus</i>	0	1	2	<i>Pardosa hortensis</i>	0	1	2
<i>Lepthyphantes tenuis</i>	0	1	2	<i>Pardosa lugubris</i>	0	1	2
<i>Lepthyphantes zimmermanni</i>	0	1	2	<i>Pardosa monticola</i>	1	1	2
<i>Leptorhoptrum robustum</i>	0	1	2	<i>Pardosa nigriceps</i>	0	1	2
<i>Linyphia hortensis</i>	0	1	2	<i>Pardosa palustris</i>	0	1	2
<i>Linyphia triangularis</i>	0	1	2	<i>Pardosa prativaga</i>	0	1	2
<i>Linyphiidae s s</i>	0	1	1	<i>Pardosa proxima</i>	0	1	2
<i>Maso sundevalli</i>	0	1	2	<i>Pardosa pullata</i>	0	1	2
<i>Meioneta beata</i>	0	1	2	<i>Pardosa saltans</i>	0	1	2
<i>Meioneta mollis</i>	0	1	2	<i>Pelecopsis parallela</i>	0	1	2
<i>Meioneta rurestris</i>	0	1	2	<i>Pelecopsis radicola</i>	1	1	0
<i>Meioneta saxatilis</i>	0	1	2	<i>Phalangium opilio</i>	0	1	1
<i>Metopobactrus prominulus</i>	1	1	2	<i>Philodromus albidus</i>	0	1	1
<i>Micaria pulcaria</i>	1	1	2	<i>Philodromus praedatus</i>	0	1	2
<i>Micaria scintillans</i>	1	1	0	<i>Phlegra fasciata</i>	1	1	2
<i>Micrargus apertus</i>	0	1	2	<i>Phrurolithus festivus</i>	0	1	2
<i>Micrargus herbigradus</i>	0	1	2	<i>Phrurolithus minimus</i>	1	1	0
<i>Micrargus rufus</i>	0	1	2	<i>Pirata hygrophilus</i>	0	1	2
<i>Micrargus subaequalis</i>	0	1	2	<i>Pirata latitans</i>	0	1	2
<i>Microlinyphia pusilla</i>	0	1	0	<i>Pirata piraticus</i>	0	1	2
<i>Microneta viaria</i>	0	1	2	<i>Pisaura mirabilis</i>	0	1	2
<i>Milleriana inerrans</i>	0	1	2	<i>Pocadicnemis juncea</i>	0	1	2
<i>Minyriolus pusillus</i>	0	1	2	<i>Pocadicnemis pumila</i>	0	1	2
<i>Mioxena blanda</i>	0	1	2	<i>Porrohomma cambridgei</i>	0	1	1
<i>Monocephalus fuscipes</i>	0	1	2	<i>Porrohomma campbelli</i>	0	1	1
<i>Myrmarachne formicaria</i>	1	1	0	<i>Porrohomma egeria</i>	0	1	1
<i>Neon reticulatus</i>	0	1	2	<i>Porrohomma errans</i>	0	1	1
<i>Neon valentulus</i>	0	1	2	<i>Porrohomma microphthalmum</i>	0	1	2
<i>Neriere clathrata</i>	0	1	2	<i>Porrohomma pygmaeum</i>	0	1	2
<i>Neriere peltata</i>	0	1	2	<i>Prinerigone vagans</i>	0	1	2
<i>Nigma flavescens</i>	0	1	0	<i>Robertus lividus</i>	0	1	2
<i>Oedothorax apicatus</i>	0	1	2	<i>Robertus neglectus</i>	0	1	2
<i>Oedothorax fuscus</i>	0	1	2	<i>Saarietia abnormis</i>	0	1	2
<i>Oedothorax gibbosus</i>	0	1	0	<i>Scotina palliardi</i>	1	1	0
<i>Oedothorax retusus</i>	0	1	2	<i>Silometopus bonessi</i>	0	1	0
<i>Ostearius melanopygius</i>	0	1	2	<i>Silometopus elegans</i>	0	1	0
<i>Oxyptila pullata</i>	0	1	1	<i>Steatoda phalerata</i>	1	2	0
<i>Ozyptila atomaria</i>	1	1	2	<i>Stemonyphantes lineatus</i>	0	1	2
<i>Ozyptila nigrita</i>	1	1	2	<i>Syedra gracilis</i>	1	1	2
<i>Ozyptila praticola</i>	0	1	2	<i>Tapinocyba insecta</i>	0	1	2
<i>Ozyptila pullata</i>	1	1	0	<i>Tapinocyba praecox</i>	0	1	2
<i>Ozyptila sanctuaria</i>	1	1	2	<i>Tapinocyboides pygmaeus</i>	1	1	1
<i>Ozyptila scabricula</i>	0	1	2	<i>Tegenaria agrestis</i>	0	1	1
<i>Ozyptila simplex</i>	0	1	2	<i>Tegenaria atrica</i>	0	1	1
<i>Ozyptila trux</i>	0	1	2	<i>Tegenaria picta</i>	0	1	1

Table A2. continued

Spiders (continued)	hab.spec	food.spec	disp
<i>Tegenaria saeva</i>	0	1	1
<i>Tegenaria silvestris</i>	0	1	1
<i>Tetragnatha montana</i>	0	1	2
<i>Tetrax denticula</i>	0	1	1
<i>Thanatus formicinus</i>	0	1	0
<i>Theridion bimaculatum</i>	0	1	2
<i>Theridion varians</i>	0	1	2
<i>Tibellus oblongus</i>	0	1	2
<i>Tiso vagans</i>	0	1	2
<i>Trichoncus saxicola</i>	1	1	0
<i>Trichopterna cito</i>	1	1	2
<i>Trochosa robusta</i>	1	1	0
<i>Trochosa rucicola</i>	0	1	2
<i>Trochosa terricola</i>	0	1	2
<i>Troxochrus cirriformis</i>	1	1	2
<i>Troxochrus scabriculus</i>	1	1	2
<i>Walckenaeria acuminata</i>	0	1	2
<i>Walckenaeria antica</i>	0	1	2
<i>Walckenaeria atrotibialis</i>	0	1	2
<i>Walckenaeria cucullata</i>	0	1	2
<i>Walckenaeria dysderoides</i>	0	1	2
<i>Walckenaeria furcillata</i>	0	1	0
<i>Walckenaeria vigilax</i>	0	1	0
<i>Xerolycosa miniata</i>	1	1	0
<i>Xerolycosa nemoralis</i>	0	1	2
<i>Xysticus acerbus</i>	1	1	1
<i>Xysticus audax</i>	0	1	1
<i>Xysticus bifasciatus</i>	1	1	1
<i>Xysticus cristatus</i>	0	1	2
<i>Xysticus erraticus</i>	1	1	2
<i>Xysticus ferrugineus</i>	0	1	1
<i>Xysticus kochi</i>	0	1	2
<i>Xysticus robustus</i>	1	1	1
<i>Zelotes latreillei</i>	0	1	0
<i>Zelotes longipes</i>	1	1	0
<i>Zelotes lutetianus</i>	0	1	0
<i>Zelotes pedestris</i>	0	1	0
<i>Zelotes petrensis</i>	1	1	0
<i>Zelotes praeficus</i>	1	1	0
<i>Zelotes pumilus</i>	0	1	0
<i>Zelotes pusillus</i>	0	1	0
<i>Zelotes serotinus</i>	1	1	0
<i>Zelotes subterraneus</i>	1	1	0
<i>Zora silvestris</i>	0	1	0
<i>Zora spinimana</i>	0	1	0

Weevils	hab.spec	food.spec	disp
<i>Acalles commutatus</i>	1	2	1
<i>Alophus triguttatus</i>	0	1	1
<i>Apion cruentatum</i>	0	2	3
<i>Apion haematodes</i>	0	3	3
<i>Baris lepidii</i>	0	2	3
<i>Barynotus obscurus</i>	0	1	1
<i>Barypeithes araneiformis</i>	0	1	1
<i>Barypeithes pellucidus</i>	0	1	1
<i>Barypeithes tenex</i>	1	1	1
<i>Brachysomus echinatus</i>	0	1	1
<i>Brachysomus hirtus</i>	1	1	1
<i>Catapion pubescens</i>	0	2	3
<i>Catapion seniculus</i>	0	2	3
<i>Ceratapion onopordi</i>	0	2	3
<i>Ceutorhynchus querceti</i>	0	3	3
<i>Comasinus setiger</i>	0	2	1
<i>Holotrichapion ononis</i>	0	2	3
<i>Hypera meles</i>	0	2	3
<i>Hypera nigrirostris</i>	0	2	3
<i>Hypera plantaginis</i>	0	2	3
<i>Hypera postica</i>	0	2	3
<i>Hypera zoilus</i>	0	2	3
<i>Ischnopterapion loti</i>	0	2	3
<i>Ischnopterapion virens</i>	0	2	3
<i>Larinus sturnus</i>	1	2	3
<i>Larinus turbinatus</i>	0	2	3
<i>Liophloeus tessulatus</i>	0	1	1
<i>Liparus coronatus</i>	0	2	1
<i>Mecinus pyraeaster</i>	0	2	3
<i>Mitoplathus caliginosus</i>	0	1	1
<i>Otiorhynchus ligneus</i>	0	1	1
<i>Otiorhynchus ligustici</i>	0	1	1
<i>Otiorhynchus ovatus</i>	0	1	1
<i>Otiorhynchus porcatus</i>	0	1	1
<i>Otiorhynchus raucus</i>	0	1	1
<i>Otiorhynchus rugosostriatus</i>	0	1	1
<i>Otiorhynchus singularis</i>	0	1	1
<i>Otiorhynchus veterator</i>	0	1	1
<i>Perapion marchicum</i>	0	3	3
<i>Phyllobius betulinus</i>	0	2	3
<i>Phyllobius pyri</i>	0	1	3
<i>Phyllobius roboretanus</i>	0	1	3
<i>Phyllobius virideaeris</i>	0	2	3
<i>Protapion apricans</i>	0	2	3
<i>Rhinoncus pericarpus</i>	0	2	3
<i>Sciaphilus asperatus</i>	0	1	1
<i>Sibinia pyrrhodactyla</i>	0	3	3
<i>Simo variegatus</i>	1	1	1
<i>Sitona hispidulus</i>	0	2	3
<i>Sitona humeralis</i>	0	2	3
<i>Sitona lepidus</i>	0	2	3
<i>Sitona lineatus</i>	0	2	3
<i>Sitona waterhousei</i>	0	2	3

Table A2. continued

Weevils (continued)	hab.spec	food.spec	disp
<i>Squamapion flavimanum</i>	1	3	3
<i>Stenopterapion tenue</i>	0	2	3
<i>Stereonychus fraxini</i>	1	3	3
<i>Strophosoma fulvicorne</i>	1	3	1
<i>Strophosoma melanogrammum</i>	0	1	1
<i>Strophosoma nebulosum</i>	1	2	1
<i>Tanymecus palliatus</i>	0	1	3
<i>Trachyploeus alternans</i>	1	3	1
<i>Trachyploeus angustisetulus</i>	0	1	1
<i>Trachyploeus aristatus</i>	1	1	1
<i>Trachyploeus asperatus</i>	1	1	1
<i>Trachyploeus bifoveolatus</i>	0	1	1
<i>Trachyploeus scabriculus</i>	0	1	1
<i>Trichosirocalus rufulus</i>	1	2	3
<i>Trichosirocalus troglodytes</i>	0	3	3
<i>Tychius picirostris</i>	0	2	3
<i>Tychius squamulatus</i>	0	3	3

Wood lice	hab.spec	body.size
<i>Androniscus dentiger</i>	1	6.5
<i>Armadillidium nasatum</i>	1	13
<i>Armadillidium opacum</i>	1	12
<i>Armadillidium pictum</i>	1	9
<i>Armadillidium pulchellum</i>	1	7
<i>Armadillidium vulgare</i>	0	17
<i>Cylisticus convexus</i>	1	14
<i>Haplotholmus mengei</i>	0	4
<i>Hyloniscus riparius</i>	1	5.5
<i>Ligidium hypnorum</i>	0	9.5
<i>Metatrichiscoides leydiggi</i>	0	3.2
<i>Oniscus asellus</i>	0	14
<i>Philoscia muscorum</i>	0	9
<i>Platyarthus hoffmannseggii</i>	1	4.5
<i>Porcellio dilatatus</i>	1	14
<i>Porcellio scaber</i>	0	13.5
<i>Porcellio spinicornis</i>	1	14
<i>Porcellionides pruinosus</i>	1	7.3
<i>Porcellium conspersum</i>	1	8
<i>Trachelipus rathkii</i>	0	13
<i>Trichoniscoides helveticus</i>	1	3.8
<i>Trichoniscus pusillus</i>	0	4
<i>Trichoniscus pygmaeus</i>	0	2.1

Millipedes	hab.spec	body.size
<i>Allajulus nitidus</i>	0	23.2
<i>Archiboreoiulus pallidus</i>	0	13.45
<i>Blaniulus guttulatus</i>	0	13.5
<i>Brachydesmus superus</i>	0	10
<i>Brachyiulus pusillus</i>	0	8.7
<i>Choneiulus palmatus</i>	0	13.5
<i>Chordeuma sylvestre</i>	0	12.9
<i>Cylindroiulus caeruleocinctus</i>	1	27.45
<i>Cylindroiulus punctatus</i>	0	22.25
<i>Glomeris intermedia</i>	0	17.5
<i>Glomeris marginata</i>	0	17.5
<i>Julus scandinavicus</i>	0	27.4
<i>Leptoiulus belgicus</i>	0	17.9
<i>Leptoiulus kervillei</i>	0	15.8
<i>Macrostermodesmus palicola</i>	0	4
<i>Melogona gallica</i>	0	9
<i>Mycogona germanica</i>	0	14.5
<i>Ommatoiulus rutilans</i>	1	34.5
<i>Ommatoiulus sabulosus</i>	1	28
<i>Ophiodesmus albonanus</i>	0	5
<i>Polydesmus angustus</i>	0	20
<i>Polydesmus coriaceus</i>	0	18
<i>Polydesmus denticulatus</i>	0	17
<i>Polydesmus inconstans</i>	0	16
<i>Polydesmus testaceus</i>	0	17.8
<i>Proteroiulus fuscus</i>	0	10.95
<i>Tachypodiulus niger</i>	0	37

Ants	hab.spec	disp
<i>Formica cunicularia</i>	1	2
<i>Formica fusca</i>	0	2
<i>Formica clara rufibarbis</i>	1	2
<i>Formica sanguinea</i>	1	0
<i>Lasius alienus</i>	1	2
<i>Lasius flavus</i>	0	2
<i>Lasius fuliginosus</i>	0	0
<i>Lasius meridionalis</i>	1	0
<i>Lasius mixtus</i>	0	0
<i>Lasius niger</i>	0	2
<i>Lasius platythorax</i>	0	2
<i>Lasius sabularum</i>	0	0
<i>Lasius umbratus</i>	0	0
<i>Myrmecina graminicola</i>	1	2
<i>Myrmica rubra</i>	0	2
<i>Myrmica ruginodis</i>	0	2
<i>Myrmica sabuleti</i>	1	2
<i>Myrmica scabrinodis</i>	0	2
<i>Myrmica schencki</i>	1	2
<i>Solenopsis fugax</i>	1	2
<i>Tapinoma erraticum subboreale</i>	1	0
<i>Temnothorax nylanderi</i>	0	2
<i>Tetramorium impurum caespitum</i>	1	2

Table A2. continued

Carabid beetles	hab. spec	troph. level	food. spec	disp	Carabid beetles (continued)	hab. spec	troph. level	food. spec	disp
<i>Abax parallelepipedus</i>	0	4	1	0	<i>Harpalus tardus</i>	0	2	1	2
<i>Abax parallelus</i>	0	4	1	0	<i>Laemostenus terricola</i>	0	4	1	0
<i>Agonum muelleri</i>	0	4	1	2	<i>Lebia chlorocephala</i>	0	4	2	0
<i>Amara aenea</i>	0	4	1	2	<i>Lebia cruxminor</i>	1	4	1	1
<i>Amara aulica</i>	0	2	1	2	<i>Leistus ferrugineus</i>	0	4	1	0
<i>Amara bifrons</i>	1	2	1	2	<i>Leistus spinibarbis</i>	0	4	1	0
<i>Amara communis</i>	0	4	1	2	<i>Loricera pilicornis</i>	0	4	2	2
<i>Amara consularis</i>	1	4	1	1	<i>Nebria brevicollis</i>	0	4	1	2
<i>Amara convexior</i>	1	2	1	2	<i>Nebria salina</i>	1	4	1	2
<i>Amara curta</i>	1	4	1	0	<i>Notiophilus biguttatus</i>	0	4	2	2
<i>Amara equestris</i>	1	2	1	2	<i>Notiophilus germinyi</i>	0	4	2	1
<i>Amara eurynota</i>	1	2	1	2	<i>Notiophilus palustris</i>	0	4	2	2
<i>Amara familiaris</i>	0	2	1	2	<i>Notiophilus rufipes</i>	0	4	2	2
<i>Amara lunicollis</i>	0	2	1	2	<i>Notiophilus substriatus</i>	0	4	2	2
<i>Amara montivaga</i>	1	2	1	0	<i>Ophonus melletii</i>	1	2	1	2
<i>Amara nitida</i>	1	2	1	0	<i>Ophonus nitidulus</i>	1	2	1	1
<i>Amara ovata</i>	1	4	1	2	<i>Ophonus puncticeps</i>	1	2	1	2
<i>Amara plebeja</i>	0	2	1	2	<i>Ophonus puncticollis</i>	1	2	1	2
<i>Amara praetermissa</i>	1	4	1	1	<i>Oxypselaphus obscurus</i>	0	4	1	0
<i>Amara similata</i>	0	2	1	2	<i>Panagaeus bipustulatus</i>	1	4	1	0
<i>Amara tibialis</i>	1	2	1	2	<i>Panagaeus cruxmajor</i>	0	4	1	0
<i>Anchomenus dorsalis</i>	0	4	1	2	<i>Paradromius linearis</i>	0	4	1	1
<i>Anisodactylus binotatus</i>	0	4	1	2	<i>Parophonus maculicornis</i>	1	2	1	0
<i>Asaphidion flavipes</i>	0	4	2	2	<i>Philorhizus melanocephalus</i>	0	4	1	2
<i>Badister bullatus</i>	0	4	1	2	<i>Poecilus cupreus</i>	0	4	1	2
<i>Badister sodalis</i>	0	4	1	0	<i>Poecilus versicolor</i>	0	4	1	2
<i>Bembidion lampros</i>	0	4	1	2	<i>Pseudoophonus rufipes</i>	0	2	1	2
<i>Bembidion obtusum</i>	0	4	1	1	<i>Pterostichus madidus</i>	0	4	1	0
<i>Bembidion properans</i>	0	4	1	2	<i>Pterostichus melanarius</i>	0	4	1	2
<i>Bembidion tetracolum</i>	0	4	1	2	<i>Pterostichus niger</i>	0	4	1	1
<i>Brachinus crepitans</i>	1	4	1	0	<i>Pterostichus nigrita</i>	0	4	1	2
<i>Calathus cinctus</i>	1	4	1	2	<i>Pterostichus ovoideus</i>	1	4	1	0
<i>Calathus fuscipes</i>	0	4	1	0	<i>Pterostichus strenuus</i>	0	4	1	2
<i>Calathus melanocephalus</i>	0	4	1	0	<i>Pterostichus vernalis</i>	0	4	1	2
<i>Calathus micropterus</i>	0	4	1	0	<i>Stenolophus teutonius</i>	0	4	1	2
<i>Carabus auratus</i>	0	4	1	0	<i>Stomis pumicatus</i>	0	4	1	0
<i>Carabus convexus</i>	1	4	1	0	<i>Syntomus foveatus</i>	1	4	1	2
<i>Carabus coriaceus</i>	0	4	1	0	<i>Syntomus truncatellus</i>	1	4	1	2
<i>Carabus monilis</i>	0	4	1	0	<i>Synuchus vivalis</i>	0	4	1	1
<i>Carabus nemoralis</i>	0	4	1	0	<i>Trechus obtusus</i>	0	4	1	2
<i>Carabus problematicus</i>	0	4	1	0	<i>Trechus quadristriatus</i>	0	4	1	2
<i>Carabus violaceus</i>	0	4	1	0	<i>Trichotichnus nitens</i>	0	4	1	0
<i>Cicindela campestris</i>	0	4	1	2	<i>Zabrus tenebrioides</i>	1	2	1	2
<i>Clivina fossor</i>	0	4	1	2					
<i>Cychrus caraboides</i>	0	4	1	0					
<i>Demetrias atricapillus</i>	0	4	1	2					
<i>Dyschirius globosus</i>	0	4	1	0					
<i>Harpalus affinis</i>	0	4	1	2					
<i>Harpalus anxius</i>	1	2	1	1					
<i>Harpalus dimidiatus</i>	1	2	1	0					
<i>Harpalus latus</i>	0	2	1	2					
<i>Harpalus rubripes</i>	0	2	1	2					
<i>Harpalus rufipalpis</i>	1	2	1	2					

Table A2. continued

True bugs	hab. spec	troph. level	food. spec	disp	True bugs (continued)	hab. spec	troph. level	food. spec	disp
<i>Acalypta carinata</i>	1	2	2	0	<i>Kalama tricornis</i>	1	2	1	1
<i>Acalypta marginata</i>	0	2	2	1	<i>Lasiacantha capucina</i>	1	2	3	0
<i>Acalypta parvula</i>	1	2	2	2	<i>Legnotus limbosus</i>	1	2	3	2
<i>Adelphocoris lineolatus</i>	0	2	1	2	<i>Leptopterna ferrugata</i>	0	2	2	0
<i>Adelphocoris quadripunctatus</i>	0	2	1	2	<i>Lygus rugulipennis</i>	0	4	1	2
<i>Adelphocoris seticornis</i>	1	4	2	2	<i>Macrotylus paykullii</i>	1	4	2	2
<i>Aelia acuminata</i>	0	2	2	2	<i>Megaloceroea recticornis</i>	0	2	2	2
<i>Aellopus atratus</i>	1	2	2	0	<i>Megalonotus antennatus</i>	1	2	1	0
<i>Agramma laetum</i>	1	2	2	1	<i>Megalonotus chiragra</i>	1	2	1	0
<i>Alydus calcaratus</i>	0	2	2	2	<i>Megalonotus dilatatus</i>	1	2	2	0
<i>Anthocoris nemoralis</i>	0	4	1	2	<i>Megalonotus praetextatus</i>	1	2	1	2
<i>Atractotomus mali</i>	0	4	2	2	<i>Megalonotus sabulicola</i>	1	2	1	2
<i>Bathysolen nubilus</i>	1	2	2	2	<i>Myrmus miriformis</i>	0	2	2	0
<i>Beosus maritimus</i>	1	2	1	2	<i>Nabis brevis</i>	1	4	1	0
<i>Berytinus clavipes</i>	1	2	2	2	<i>Nabis ericetorum</i>	0	4	1	0
<i>Berytinus hirticornis</i>	1	4	1	2	<i>Nabis ferus</i>	0	4	1	2
<i>Berytinus minor</i>	1	4	1	2	<i>Nabis flavomarginatus</i>	0	4	1	0
<i>Berytinus signoreti</i>	1	2	2	0	<i>Nabis limbatus</i>	0	4	1	0
<i>Campylomma verbasci</i>	0	4	1	2	<i>Nabis pseudoferus</i>	0	4	1	0
<i>Campyloneura virgula</i>	0	4	1	2	<i>Nabis rugosus</i>	0	4	1	0
<i>Campylosteira verna</i>	1	2	2	1	<i>Odontoscels fuliginosa</i>	1	2	1	1
<i>Capsus ater</i>	0	2	2	2	<i>Orius niger</i>	0	4	1	2
<i>Catoplatys fabricii</i>	1	2	3	1	<i>Orthocephalus coriaceus</i>	1	2	2	0
<i>Ceraleptus lividus</i>	1	2	2	2	<i>Orthocephalus saltator</i>	1	2	2	0
<i>Ceratocombus coleoptratus</i>	0	4	1	2	<i>Ortholomus punctipennis</i>	1	2	1	2
<i>Chlamydatus saltitans</i>	1	4	1	2	<i>Palomena prasina</i>	0	2	1	2
<i>Coranus subapterus</i>	0	4	1	0	<i>Peritrechus geniculatus</i>	0	2	1	2
<i>Coreus marginatus</i>	0	2	1	2	<i>Phytocoris pini</i>	0	4	2	2
<i>Coriomeris denticulatus</i>	1	2	2	2	<i>Phytocoris varipes</i>	0	4	1	2
<i>Derephysia sinuotocollis</i>	0	2	3	0	<i>Pithanus maerkelii</i>	0	2	1	0
<i>Dicyphus annulatus</i>	1	4	2	2	<i>Plagiognathus chrysanthemi</i>	0	4	1	2
<i>Dolycoris baccarum</i>	0	2	1	2	<i>Plinthisus brevipennis</i>	0	2	1	1
<i>Drymus brunneus</i>	0	2	1	0	<i>Podops inuncta</i>	1	2	2	2
<i>Drymus latus</i>	1	2	1	1	<i>Prostemma guttula</i>	1	4	2	0
<i>Drymus ryeii</i>	0	2	1	0	<i>Psallus falleni</i>	0	4	3	2
<i>Drymus sylvaticus</i>	0	2	1	0	<i>Rhaphigaster nebulosa</i>	0	4	1	2
<i>Emblethis verbasci</i>	1	2	1	2	<i>Rhopalus subrufus</i>	0	2	1	2
<i>Eremocoris plebejus</i>	0	2	2	2	<i>Rhyparochromus phoeniceus</i>	1	2	1	2
<i>Eremocoris podagricus</i>	1	2	1	1	<i>Rhyparochromus pini</i>	1	2	1	2
<i>Europiella alpina</i>	1	2	3	2	<i>Saldula orthochila</i>	0	4	1	0
<i>Eurygaster maura</i>	1	2	2	2	<i>Saldula saltatoria</i>	0	4	1	0
<i>Eurygaster testudinaria</i>	0	2	2	2	<i>Sciocoris cursitans</i>	1	2	1	2
<i>Gampsocoris punctipes</i>	1	4	1	2	<i>Scolopostethus affinis</i>	0	2	1	2
<i>Geocoris grylloides</i>	1	4	1	0	<i>Scolopostethus grandis</i>	0	2	1	2
<i>Globiceps fulvicollis</i>	0	4	1	0	<i>Scolopostethus puberulus</i>	1	2	1	2
<i>Graptopeltus lynceus</i>	1	2	1	2	<i>Scolostethus thomsoni</i>	0	2	1	1
<i>Halticus apterus</i>	1	2	1	0	<i>Sehirus luctuosus</i>	1	2	2	2
<i>Halticus saltator</i>	0	2	1	0	<i>Stygnocoris fuliginus</i>	1	2	1	2
<i>Heterocordylus genistae</i>	1	4	3	2	<i>Stygnocoris rusticus</i>	1	2	1	0
<i>Himacerus boops</i>	0	4	1	0	<i>Stygnocoris sabulosus</i>	1	2	1	2
<i>Himacerus major</i>	0	4	1	2	<i>Syromastus rhombeus</i>	1	2	2	2
<i>Himacerus mimicoides</i>	0	4	1	2	<i>Tropistethus holosericus</i>	1	2	1	0
<i>Holcostethus strictus</i>	0	4	1	2	<i>Zicrona caerulea</i>	0	4	1	2

Table A2. continued

Vascular plants	disp	hab. spec	Vascular plants (continued)	disp	hab. spec	Vascular plants (continued)	disp	hab. spec
<i>Acer species</i>	1	0	<i>Clinopodium vulgare</i>	1	1	<i>Hieracium pilosella</i>	1	0
<i>Achillea millefolium</i>	1	0	<i>Coeloglossum viride</i>	1	0	<i>Hieracium sabaudum</i>	1	0
<i>Agrimonia eupatoria</i>	1	1	<i>Convolvulus arvensis</i>	1	0	<i>Hieracium umbellatum</i>	1	0
<i>Agrostis capillaris</i>	1	0	<i>Conyza canadensis</i>	1	0	<i>Holcus lanatus</i>	1	0
<i>Agrostis stolonifera</i>	1	0	<i>Cornus sanguinea</i>	1	0	<i>Holcus mollis</i>	1	0
<i>Agrostis vinealis</i>	1	1	<i>Corylus avellana</i>	1	0	<i>Hypericum dubium</i>	0	0
<i>Aira caryophyllea</i>	1	1	<i>Crataegus monogyna</i>	1	0	<i>Hypericum maculatum</i>	0	0
<i>Aira praecox</i>	1	1	<i>Crepis biennis</i>	0	0	<i>Hypericum perforatum</i>	0	0
<i>Ajuga reptans</i>	0	0	<i>Crepis capillaris</i>	1	0	<i>Hypochaeris radicata</i>	1	0
<i>Allium vineale</i>	0	0	<i>Cuscuta epithymum</i>	1	0	<i>Inula conyzae</i>	1	0
<i>Anagallis arvensis</i>	0	0	<i>Cymbalaria muralis</i>	0	0	<i>Jasione montana</i>	1	1
<i>Anisantha sterilis</i>	1	0	<i>Cynosurus cristatus</i>	1	0	<i>Juncus compressus</i>	1	0
<i>Anthoxanthum odoratum</i>	1	0	<i>Cytisus scoparius</i>	0	0	<i>Kickxia elatine</i>	0	0
<i>Anthyllis vulneraria</i>	1	1	<i>Dactylis glomerata</i>	1	0	<i>Knautia arvensis</i>	1	1
<i>Aphanes arvensis</i>	1	0	<i>Dactylorhiza maculata</i> subsp. <i>fuchsii</i>	1	1	<i>Koeleria macrantha</i>	1	0
<i>Arabidopsis thaliana</i>	1	0				<i>Koeleria pyramidata</i>	1	1
<i>Arabis hirsuta</i>	1	0	<i>Danthonia decumbens</i>	1	1	<i>Lamium purpureum</i>	0	0
<i>Arenaria serpyllifolia</i>	1	0	<i>Daucus carota</i>	1	0	<i>Lapsana communis</i>	1	0
<i>Arrhenatherum elatius</i>	1	0	<i>Diplotaxis muralis</i>	1	0	<i>Lathyrus pratensis</i>	0	0
<i>Bellis perennis</i>	1	0	<i>Echium vulgare</i>	1	0	<i>Leontodon autumnalis</i>	1	0
<i>Betula pubescens</i>	1	0	<i>Elytrigia repens</i>	1	0	<i>Leontodon hispidus</i>	1	1
<i>Brachypodium pinnatum</i>	1	1	<i>Erigeron acer</i>	1	0	<i>Leontodon saxatilis</i>	1	0
<i>Briza media</i>	0	1	<i>Euphrasia stricta</i>	0	1	<i>Leucanthemum vulgare</i>	1	1
<i>Bromus hordeaceus</i>	1	0	<i>Fallopia convolvulus</i>	1	0	<i>Linaria vulgaris</i>	1	0
<i>Bryonia dioica</i>	1	0	<i>Festuca arundinacea</i>	1	0	<i>Linum catharticum</i>	1	1
<i>Bunium bulbocastanum</i>	1	1	<i>Festuca filiformis</i>	1	0	<i>Listera ovata</i>	1	0
<i>Calamagrostis epigejos</i>	1	0	<i>Festuca pratensis</i>	1	0	<i>Lolium perenne</i>	1	0
<i>Calluna vulgaris</i>	1	0	<i>Festuca rubra</i>	1	0	<i>Lotus corniculatus</i>	1	0
<i>Calystegia sepium</i>	1	0	<i>Fragaria vesca</i>	1	0	<i>Luzula campestris</i>	1	0
<i>Campanula rotundifolia</i>	1	1	<i>Fraxinus excelsior</i>	1	0	<i>Malus sylvestris</i>	1	0
<i>Capsella bursa pastoris</i>	1	0	<i>Galeopsis tetrahit</i>	1	0	<i>Malva moschata</i>	1	0
<i>Carduus nutans</i>	1	0	<i>Galium aparine</i>	1	0	<i>Medicago falcata</i>	1	0
<i>Carex caryophyllea</i>	1	1	<i>Galium mollugo</i>	0	0	<i>Medicago lupulina</i>	1	0
<i>Carex flacca</i>	1	1	<i>Galium pumilum</i>	1	1	<i>Medicago sativa</i>	1	0
<i>Carex pallescens</i>	1	0	<i>Galium verum</i>	0	0	<i>Melampyrum arvense</i>	1	0
<i>Carex panicea</i>	1	0	<i>Genista tinctoria</i>	0	1	<i>Melampyrum pratense</i>	0	0
<i>Carex spicata</i>	1	0	<i>Gentianella ciliata</i>	0	1	<i>Melilotus albus</i>	0	0
<i>Carex sylvatica</i>	1	0	<i>Gentianella germanica</i>	0	1	<i>Melilotus altissimus</i>	0	0
<i>Carlina vulgaris</i>	0	1	<i>Geranium columbinum</i>	1	0	<i>Myosotis arvensis</i>	1	0
<i>Caucalis platycarpos</i>	1	0	<i>Geranium dissectum</i>	1	0	<i>Ononis repens</i>	0	1
<i>Centaurea jacea</i>	1	0	<i>Geranium molle</i>	1	0	<i>Ophrys apifera</i>	1	1
<i>Centaurea scabiosa</i>	1	1	<i>Geranium robertianum</i>	1	0	<i>Orchis morio</i>	1	1
<i>Centaureum erythraea</i>	1	1	<i>Geum urbanum</i>	1	0	<i>Origanum vulgare</i>	0	1
<i>Cerastium arvense</i>	1	0	<i>Glechoma hederacea</i>	0	0	<i>Papaver rhoeas</i>	0	0
<i>Cerastium fontanum</i>	1	0	<i>Gymnadenia conopsea</i>	1	1	<i>Phleum pratense</i>	1	0
<i>Cerastium semidecandrum</i>	1	0	<i>Hedera helix</i>	1	0	<i>Picris hieracioides</i>	1	0
<i>Chaerophyllum temulum</i>	0	0	<i>Helianthemum nummularium</i>	1	1	<i>Pimpinella saxifraga</i>	1	1
<i>Chenopodium polyspermum</i>	1	0	<i>Helictotrichon pratense</i>	1	1	<i>Pinus sylvestris</i>	1	0
<i>Cirsium acaule</i>	0	1	<i>Helictotrichon pubescens</i>	1	1	<i>Plantago lanceolata</i>	1	0
<i>Cirsium arvense</i>	1	0	<i>Heracleum sphondylium</i>	1	0	<i>Plantago major</i>	1	0
<i>Cirsium vulgare</i>	1	0	<i>Hieracium caespitosum</i>	1	0	<i>Plantago media</i>	1	1
<i>Clematis vitalba</i>	1	0	<i>Hieracium laevigatum</i>	0	0	<i>Platanthera bifolia</i>	1	1

Table A2. continued

Vascular plants (continued)	disp	hab. spec	Vascular plants (continued)	disp	hab. spec
<i>Platanthera chlorantha</i>	1	1	<i>Teucrium chamaedrys</i>	1	0
<i>Poa angustifolia</i>	1	1	<i>Thymus pulegioides</i>	1	1
<i>Poa compressa</i>	1	0	<i>Thymus vulgaris</i>	1	0
<i>Poa pratensis</i>	1	0	<i>Tragopogon pratensis</i>	1	0
<i>Poa trivialis</i>	1	0	<i>Trifolium dubium</i>	1	0
<i>Polygala vulgaris</i>	0	1	<i>Trifolium medium</i>	1	0
<i>Polygonum aviculare</i>	1	0	<i>Trifolium pratense</i>	1	0
<i>Potentilla anserina</i>	1	0	<i>Trifolium repens</i>	1	0
<i>Potentilla erecta</i>	1	1	<i>Trisetum flavescens</i>	1	1
<i>Potentilla sterilis</i>	1	0	<i>Ulmus species</i>	1	0
<i>Potentilla verna</i>	1	1	<i>Urtica dioica</i>	1	0
<i>Primula veris</i>	0	1	<i>Valeriana officinalis</i>	1	0
<i>Prunella vulgaris</i>	1	0	<i>Verbascum thapsus</i>	0	0
<i>Prunus avium</i>	1	0	<i>Veronica chamaedrys</i>	1	0
<i>Prunus spinosa</i>	1	0	<i>Viburnum opulus</i>	1	0
<i>Quercus robur</i>	1	0	<i>Vicia cracca</i>	0	0
<i>Quercus rubra</i>	1	0	<i>Vicia sativa</i>	0	0
<i>Rhamnus species</i>	1	0	<i>Viola canina</i>	0	0
<i>Ranunculus acris</i>	0	0	<i>Viola hirta</i>	0	0
<i>Ranunculus bulbosus</i>	0	0			
<i>Ranunculus polyanthemos</i>	0	0			
<i>Ranunculus repens</i>	1	0			
<i>Reseda lutea</i>	0	0			
<i>Rhinanthus alectorolophus</i>	1	1			
<i>Rhinanthus angustifolius</i>	1	0			
<i>Rhinanthus minor</i>	1	1			
<i>Rosa species</i>	1	0			
<i>Rubus species</i>	1	0			
<i>Rumex acetosa</i>	1	0			
<i>Rumex acetosella</i>	1	0			
<i>Rumex crispus</i>	1	0			
<i>Rumex obtusifolius</i>	1	0			
<i>Salvia pratensis</i>	1	0			
<i>Salvia verticillata</i>	1	1			
<i>Sambucus nigra</i>	1	0			
<i>Sanguisorba minor</i>	1	1			
<i>Sanguisorba officinalis</i>	1	0			
<i>Scabiosa columbaria</i>	1	1			
<i>Senecio erucifolius</i>	1	0			
<i>Senecio jacobaea</i>	1	0			
<i>Silene vulgaris</i>	1	1			
<i>Sisymbrium officinale</i>	0	0			
<i>Solanum nigrum</i>	1	0			
<i>Sonchus asper</i>	1	0			
<i>Sonchus oleraceus</i>	1	0			
<i>Spiranthes spiralis</i>	1	1			
<i>Stachys officinalis</i>	1	1			
<i>Stellaria graminea</i>	1	0			
<i>Stellaria media</i>	1	0			
<i>Succisa pratensis</i>	1	0			
<i>Taraxacum officinale</i>	1	0			
<i>Tetragonolobus maritimus</i>	1	0			

Appendix 4. Results permanova tests

Table A3. Results of the adonis analyses to test for relationships between species traits and the response of species in terms of delta deviance, a measure of homogenization or differentiation, for each taxonomic group. Significant results ($p < 0.05$) are shown in bold.

Group	Traits	Df	SumsSquare	R ²	p
Plants (n = 223)	Dispersal	1	2.221	0.001	0.791
	Habitat affinity	1	1.290	0.000	0.817
	Dispersal:Habitat affinity	1	11.777	0.004	0.444
	Residuals	219	3352.774	0.995	
Weevils (n = 54)	Food specialist	1	118.220	0.064	0.070
	Dispersal	1	1.960	0.001	0.812
	Habitat affinity	1	0.110	0.000	0.958
	Food specialist:Dispersal	1	19.030	0.010	0.493
	Food specialist:Habitat affinity	1	26.940	0.015	0.419
	Dispersal:Habitat affinity	1	37.820	0.020	0.330
	Residuals	47	1649.440	0.890	
True bugs (n = 61)	Habitat affinity	1	53.550	0.029	0.213
	Trophic level	1	32.170	0.018	0.321
	Dispersal	1	35.740	0.020	0.298
	Food specialist	1	24.260	0.013	0.383
	Habitat affinity:Trophic level	1	25.490	0.014	0.368
	Habitat affinity:Dispersal	1	15.860	0.009	0.479
	Habitat affinity:Food specialist	1	5.760	0.003	0.665
	Trophic level:Dispersal	1	0.010	0.000	0.985
	Trophic level:Food specialist	1	7.790	0.004	0.640
	Dispersal:Food specialist	1	8.430	0.005	0.606
	Residuals	50	1613.140	0.885	
Ants (n = 23)	Habitat affinity	1	1.810	0.005	0.734
	Dispersal	1	0.040	0.000	0.967
	Habitat affinity:Dispersal	1	0.680	0.002	0.862
	Residuals	19	358.720	0.993	
Carabid beetles (n = 91)	Trophic level	1	37.990	0.019	0.184
	Dispersal	1	26.170	0.013	0.275
	Habitat affinity	1	0.690	0.000	0.842
	Trophic level:Dispersal	1	0.280	0.000	0.903
	Trophic level:Habitat affinity	1	0.000	0.000	0.986
	Dispersal:Habitat affinity	1	14.980	0.007	0.414
	Residuals	84	1953.900	0.961	
Spiders (n = 151)	Habitat affinity	1	53.800	0.010	0.217
	Dispersal	1	11.700	0.002	0.574
	Food specialist	1	11.300	0.002	0.584
	Habitat affinity:Dispersal	1	246.600	0.044	0.011
	Habitat affinity:Food specialist	1	23.400	0.004	0.456
	Dispersal:Food specialist	1	35.100	0.006	0.351
	Residuals	144	5206.600	0.932	
Millipedes (n = 25)	Body size	1	1.970	0.004	0.793
	Habitat affinity	1	0.830	0.002	0.874
	Body size:Habitat affinity	1	13.010	0.024	0.523
	Residuals	20	536.780	0.971	
Wood lice (n = 10)	Body size	1	39.489	0.162	0.162
	Habitat affinity	1	63.562	0.261	0.063
	Body size:Habitat affinity	1	61.322	0.252	0.104
	Residuals	6	79.176	0.325	

Table A4. Results of the adonis analyses to test for relationships between species traits and the response of species in terms of occupancy change for each taxonomic group. Significant results ($p < 0.05$) are shown in bold.

Group	Traits	Df	SumsSquare	R ²	p
Plants (n = 223)	Habitat affinity	1	0.022	0.003	0.444
	Dispersal	1	0.009	0.001	0.673
	Habitat affinity:Dispersal	1	0.133	0.018	0.060
	Residuals	219	7.281	0.978	
Weevils (n = 54)	Food specialist	1	0.307	0.089	0.024
	Habitat affinity	1	0.058	0.017	0.341
	Dispersal	1	0.001	0.000	0.885
	Food specialist:Habitat affinity	1	0.005	0.001	0.793
	Food specialist:Dispersal	1	0.015	0.004	0.632
	Habitat affinity:Dispersal	1	0.019	0.006	0.569
	Residuals	47	3.055	0.883	
True bugs (n = 61)	Trophic level	1	0.142	0.062	0.057
	Food specialist	1	0.064	0.028	0.211
	Habitat affinity	1	0.036	0.016	0.320
	Dispersal	1	0.029	0.013	0.412
	Trophic level:Habitat affinity	1	0.028	0.012	0.406
	Habitat affinity:Dispersal	1	0.052	0.023	0.250
	Food specialist:Habitat affinity	1	0.000	0.000	0.928
	Trophic level:Dispersal	1	0.005	0.002	0.714
	Trophic level:Food specialist	1	0.019	0.008	0.461
	Food specialist:Dispersal	1	0.000	0.000	0.983
	Residuals	50	1.918	0.836	
Ants (n = 23)	Dispersal	1	0.095	0.068	0.200
	Habitat affinity	1	0.115	0.082	0.201
	Dispersal:Habitat affinity	1	0.059	0.042	0.327
	Residuals	19	1.137	0.808	
Carabid beetles (n = 91)	Trophic level	1	0.171	0.025	0.136
	Habitat affinity	1	0.057	0.008	0.428
	Dispersal	1	0.005	0.001	0.794
	Trophic level:Habitat affinity	1	0.019	0.003	0.636
	Trophic level:Dispersal	1	0.078	0.011	0.307
	Habitat affinity:Dispersal	1	0.000	0.000	0.932
	Residuals	84	6.627	0.952	
Spiders (n = 151)	Habitat affinity	1	0.407	0.036	0.026
	Food specialist	1	0.004	0.000	0.804
	Dispersal	1	0.002	0.000	0.875
	Habitat affinity:Food specialist	1	0.021	0.002	0.588
	Habitat affinity:Dispersal	1	0.007	0.001	0.743
	Food specialist:Dispersal	1	0.058	0.005	0.373
	Residuals	144	10.796	0.956	
Millipedes (n = 25)	Body size	1	0.070	0.025	0.500
	Habitat affinity	1	0.026	0.009	0.673
	Body size:Habitat affinity	1	0.028	0.010	0.674
	Residuals	20	2.653	0.955	
Wood lice (n = 10)	Body size	1	0.563	0.702	0.003
	Habitat affinity	1	0.036	0.045	0.306
	Body size:Habitat affinity	1	0.016	0.020	0.509
	Residuals	6	0.187	0.233	



Ant hills form valuable microhabitats (Photo: Toos van Noordwijk)

Chapter 3

Life-history strategies as a tool to identify conservation constraints: A case-study on ants in chalk grasslands

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Abstract

Species' life-history traits underlie species-environment relationships. Therefore, analysis of species traits, combined into life-history strategies, can be used to identify key factors shaping the local species composition. This is demonstrated in a case-study on ants in chalk grasslands. We developed four life-history strategies based on traits related to reproduction, development, dispersal and synchronization that are documented in the literature. These theoretical strategies reflect different responses to certain environmental conditions. They can be characterized as generalists (G), poor dispersers (D), species whose distribution is limited to sites with high food availability (F) and species that are restricted to sites with high soil temperatures during nest founding (I). Next, we tested whether the occurrence of these strategies differed between six Dutch chalk grasslands and four reference sites situated in Germany and Belgium. We found significant differences in species numbers between sites for strategies D and I but not for strategies F and G. The differences could be explained by differences in connectivity and microhabitat conditions; species richness of strategy D decreased exponentially with increasing distance to the next nearest chalk grassland, while summer soil temperature strongly affected species richness of strategy I. From these relationships we could successfully identify the most relevant bottlenecks for the occurrence of both of these strategies in Dutch chalk grasslands. Management recommendations resulting from this analysis include adapting the management timing in Dutch chalk grasslands and focussing on counteracting habitat isolation. With this case-study we demonstrate that the life-history strategy approach is a valuable alternative to approaches that try to identify key factors by analysing the variation in environmental parameters. The main advantage of the presented alternative is the focus on mechanistically understanding species responses, allowing a comparison of processes rather than occurrences of single species.

Keywords

Reproduction tactic, Formicidae, species traits, restoration, habitat isolation, dispersal, microclimate

Nomenclature follows Seifert 2007.

Introduction

To assess the success rate of restoration and conservation projects, restored sites are frequently compared to more pristine reference sites, either in space or time (White and Walker 1997). In this way the extent to which the target sites differ from reference sites can be determined, for example in terms of species richness or abundance of characteristic species. To define successful management measures it is essential to establish which factor is key in explaining these differences between target sites and reference sites. The most common method to get insight in these species-environment relationships is a top-down approach in which the variation in environmental parameters is analysed and correlated to differences in species composition by use of multivariate statistics. Such top-down approaches have been proven to be a valuable tool to explore which factors out of the multitude of measured ones could potentially be causing the observed difference. However, they present two major problems. First, such correlations cannot be used to establish causality (Verberk 2010; Michener 1997), while causal understanding is essential to predict which actions will be most effective for reaching management targets (Bradshaw 1996; Hobbs and Norton 1996). Secondly when using these top-down approaches, researchers have to decide in advance which factors they will measure. Especially in complex restoration situations, the number of possible factors to measure is overwhelming. Many general factors like microclimate, fragmentation and management practice can be measured in different ways and at different levels of detail, all with a (slightly) different outcome as a result. Selecting in advance which factors to measure essentially prevents the discovery of new key factors, limiting the value of applied restoration and conservation ecology to advance our understanding regarding more fundamental aspects of community ecology.

In recent years a growing number of studies have demonstrated that species' life-history traits can successfully be used to gain insight in species-environment relationships (Bremner et al. 2006; Cristofoli et al. 2010; McGill et al. 2006). This provides a bottom-up (starting at the species end of species-environment relationships) alternative to traditional top-down approaches (Verberk et al. 2008b). Species traits include any morphological, physiological or phenological feature without reference to the environment (Violle et al. 2007). The attractiveness of trait-based approaches is rooted in the promise of traits potentially providing mechanistic understanding of species-environment relationships. This makes them especially appealing to explain and predict species responses to changes in their environment (e.g. Van Kleef et al. 2006; Verberk et al. 2010a; Williams et al. 2010). Previous trait-based approaches have mostly tried to link individual traits to species' responses. However, within species, traits are not independent but are linked to form an integrated response to particular ecological problems (Siepel 1994; Siepel 1995; Stearns 1976). Traits are interconnected through trade-offs and different traits may act in concert (Siepel 1994; Verberk et al. 2008a). Therefore a specific trait may have very different ecological implications depending on the remainder of the traits possessed by the species. E.g. wings generally make an ant species more mobile, but if flight is used only to find mates while the founding of a new nest occurs by nest-splitting (walking to a new site accompanied by workers), the presence of wings is of no value to the species' colonization ability. The importance of these linkages between traits is widely acknowledged, however, only few studies have found a way to deal with them. Siepel (1994), Verberk et al. (2008a)

and Van Turnhout et al. (2012) have found an alternative by operationalising species traits through life-history strategies (called tactics in Siepel 1994). They focused on trait combinations rather than single traits, allowing to evaluate the relative importance of traits and to weight traits in an informed way depending on the remainder of a species' biology. In this way they assigned species to different life-history strategies that respond in a uniform way to changes in their environment.

In this paper we develop such life-history strategies for ants in chalk grasslands and demonstrate that life-history strategies can be used as indicators for specific ecological processes within a conservation context. In line with the components of life-history strategies identified by Siepel (1994) and Verberk et al. (2008a) we focus on traits related to development, reproduction, dispersal and synchronization to build life-history strategies. Since ants live in eusocial colonies which act as single reproductive units (Hölldobler and Wilson 1990) we focus on colony development and colony reproductive effort rather than individual development and reproduction. Ants are especially suitable for a life-history strategy approach as both the general life-cycle and deviations from it are well documented (Hölldobler and Wilson 1990; Seifert 2007). In addition species traits of ants are strongly interrelated (Bourke and Franks 1995; Tschinkel 1991) and especially the mode of nest founding is connected to numerous other traits (Bourke and Franks 1995; Johnson 2006). Nest founding is also widely recognized to be the most vulnerable and critical period in the life-cycle of an ant colony (Hölldobler and Wilson 1990; Johnson 2006). Therefore, it is reasonable to assume that the combination of life-history traits related to the nest founding phase most strongly determine under which conditions species can survive. This makes the nest founding mode a good starting point when exploring the differences in life-history strategy between ant species.

Chalk grasslands in North-Western Europe are potentially very rich in flora and fauna (WallisDeVries et al. 2002) including ants (Dekoninck et al. 2007; Seifert 2007). Over the past century however, the number, size and quality of these grasslands have declined strongly (WallisDeVries et al. 2002). This decline has been especially severe in the Netherlands, where only 20 chalk grassland sites remain with a combined surface area of no more than 30 ha. (Willems 2001). These sites are highly isolated and have suffered from eutrophication from both adjacent agricultural areas and airborne nitrogen pollution. Together with the cessation of traditional land use, this has resulted in severe grass- and shrub encroachment by the early 1980's (Bobbink and Willems 1993; Willems 2001). At this point populations of characteristic ant species had also declined in the Dutch chalk grasslands (De Boer 1983; Mabelis 1983). In the ensuing decades restoration management has been implemented or improved, focusing primarily on removing excess primary production through grazing, mowing or both. To evaluate the current status of the ant assemblages in these habitats, we sampled ants in six of the largest Dutch chalk grasslands and four reference sites in Belgium and Germany. Specifically, the aim of this study is to: 1) develop life-history strategies for ants based on literature data to predict which environmental factors are of key importance; 2) test whether these predictions correspond to observed differences in environmental conditions between sampling locations using independent field data and; 3) use this mechanistic understanding of species-environment relationships to formulate management recommendations to improve the status of the ant fauna in the study sites.

Methods

Study sites

Ants were sampled in six Dutch chalk grasslands and in one Belgian and three German reference sites (Figure 1). The German and Belgian sites were selected because they were expected to host more ant species that are characteristic for chalk grasslands and are thus presumably more intact with respect to factors that are important for these ant species. In general the reference sites are either less isolated or have been less degraded due to a shorter period of abandonment, lower atmospheric nitrogen levels or more effective restoration management. However, both among and between the Dutch sites and the reference sites there are considerable differences with respect to size, slope, aspect, degree of isolation and current and past management type and timing (Table 1). In addition, management history was not known in great detail for all sites. To quantify the combined effect of slope, aspect and management on the soil temperature we used Askey Keytag data loggers (model KTL-108). Due to logistical reasons no loggers were placed in the German sites. Soil temperature was measured at 30 minute intervals at all sampled locations (see Field sampling) in the Netherlands and Belgium throughout the year. Loggers were sealed in a plastic bag and buried at a depth of 5 cm (sensor depth). These measurements were conducted in 2008, while ant sampling took place in 2005 and 2006. However, as the management regime in all sites follows a strict yearly cycle the relative differences between sites should correspond well between years. Two sampling locations where the management in 2008 differed from previous years were excluded from the temperature data analysis. Unfortunately there was considerable drop out of data loggers as a result of management activity, failing loggers and logger disappearance. This made it impossible to compare large periods of time between sites. As an alternative we selected five warm days between May and November with maximum logger data availability to compare soil temperatures between sites. To select these warm days we used weather data from the Maastricht weather station published at www.meteomaastricht.nl.

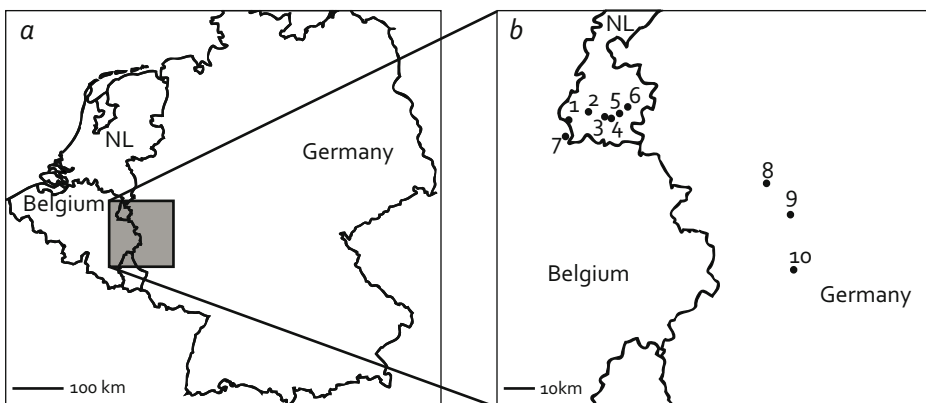


Figure 1. Location of the study area in North-Western Europa (a.) and the study sites within this region (b). 1 Sint Pietersberg (SP), 2 Bemelerberg (Bem), 3 Laamhei (Laa), 4 Berghofweide (Bh), 5 Wrakelberg (Wra), 6 Kunderberg (Kun), 7 Thier de Lanaye (Thi), 8 Bürvenicherberg (Bu), 9 Halsberg (Ha), 10 Ahrhütte (Ah).

Table 1. Main characteristics of the sampling locations in the Netherlands (NL), Belgium (BE) and Germany (GER). The degree of isolation is defined as the distance to the next nearest chalk grassland. The management period is depicted as the months from January to December in which management is executed (white).

Site	Country	Size (ha)	Aspect	Inclination (°)	Isolation (km)	Management	Management period
Bemelerberg (Bem)	NL	5.2	SSW-SSE	20-30	0.3	Grazing	JASON
Berghofweide (Bh)	NL	2.6	S	10-15	1.2	Mowing & grazing	JASON
Laamhei (Laa)	NL	1.3	W-WNW	10-15	1.2	Grazing	JASON
Kunderberg (Kun)	NL	2.9	SW	15-20	3.0	Grazing	JASON
Sint Pietersberg (SP)	NL	3.2	S/W	15-25	1.0	Grazing	FMAMJASON
Wrakelberg (Wra)	NL	4.7	S	15-20	1.0	Mowing	JASON
Thier de Lanaye (Thi)	BE	4.0	S-SE-ENE	20-30	0.8	Grazing	AMJASON
Bürvenicherberg (Bu)	GER	2.6	SSW-SE	15-25	0.3	Grazing	AMJJ
Ahrhütte (Ah)	GER	4.3	NW-S-SE	15-25	0.1	Grazing	AMJJ
Halsberg (Ha)	GER	11.2	SSE	15-25	0.5	Grazing	AMJJ

All selected days were (almost) dry with a minimum of cloud cover and an average and maximum daily temperature well above the long-term monthly average (derived from the Dutch Meteorological Institute KNMI available at www.knmi.nl). We selected warm days as the differences in soil temperature between sites are most pronounced on these days.

Field sampling

Ant sampling was conducted using four series of pitfall traps per site. Each series consisted of five traps with an 8.5 cm diameter which were placed approximately 5 meters apart. Each trap was covered with a 10 cm by 10 cm wooden plate placed at a height of about 2 cm above the ground to reduce evaporation. Traps were filled with 0.1 L formaldehyde solution (5%) to which a few drops of liquid soap were added to reduce surface tension. The four pitfall trap series per site were placed at least 25 meters (but mostly more) apart and together sampled the main variation in aspect, inclination and vegetation structure within each chalk grassland. In general, this within-site variation was rather limited. At Bemelerberg, Laamhei, Kunderberg, Wrakelberg, Ahrhütte, Halsberg and Thier de Lanaye sampling was carried out from the beginning of July 2005 until the end of October 2005. Sint Pietersberg, Berghofweide and Bürvenicherberg were sampled from the beginning of July 2006 until the end of October 2006. Traps were serviced every three weeks during the sampling period. Ant nests usually exist for several years (Seifert 2007) and as there were no recent management changes within sites, no difference is expected between consecutive years. Ants were identified to the species level by the second author, using Boer (2010) and Seifert (2007). Pitfall trap data are not suitable to measure local nest density in ants, as the number of individuals caught is strongly influenced by the proximity of the nest (Schlick-Steiner et al. 2006). Therefore, only species presence and absence per pitfall trap series was recorded.

Trait selection

Traits were obtained from published literature for all species found in our study. All species traits falling within the four domains (reproduction, development, synchronization and dispersal) defined by Stearns (1976) and Siepel (1994) that were reported by Hölldobler and Wilson (1990) to play a role in the life-cycle of ants were considered. Selecting for traits that play a role at the population level and that actually differed between the species in our study, the following life-history traits were incorporated: main mode of nest founding, additional nest founding modes, mode of colony growth, mature nest size, maximum colony age, development speed of worker larvae, development stages capable of overwintering, number of males and gynes produced, costs of producing a single gyne, mode of dispersal prior to nest foundation, timing of the nuptial flight, period of initial egg-laying and period of larval development. Feeding niche was not considered separately as the differences in diet choice and diet breadth were very limited among the studied species (Seifert 2007).

Life-history strategies

Life-history strategies were derived by starting with the main nest founding mode. For all nest founding modes represented by species in our study it was deduced from literature what the ecological consequences are and thus under which environmental conditions species with this trait are favoured or selected against. Next, it was analysed for each nest founding mode which other traits co-occur and what the consequences of these trait combinations are. Specifically it was analysed what combinations of traits could counter or amplify the ecological consequences of the main nest founding mode and what new limitations arise from these additional traits. At the end of this exercise all species with similar ecological responses were grouped into the same life-history strategy, thus partially grouping species differing in some single traits. In this way we created a limited number of functionally different life-history strategies with clear predictions with respect to their response to specific environmental factors.

Data analysis

For each of the identified strategies we tested whether the number of species per pitfall trap series differed between sites using a Kruskal-Wallis test. For each strategy that showed a significant difference in the number of species per site we best fitted regression curves between the number of species and specific environmental factors, using the Akaike information criterion (AIC). The choice for environmental factors to be included followed the species-environment relationships predicted from the theoretically derived life-history strategies. In addition we explored the effect of the management regime on the changes in soil temperature during the summer season. Using an ANOVA we tested whether the soil temperature on a warm day in spring (May 12) and summer (August 6) differed between sites where vegetation was removed in summer (summer management; Table 1) and sites where management was only executed in autumn and winter. Likewise we tested whether the change in soil temperature between these dates differed between sites with and without summer management.

Results

Life-history strategies

In total 35 ant species were caught. The life-history traits of these species are listed in Appendix 1. There were four main modes of colony founding: (i) nest-splitting, (ii) social parasitism, (iii) semi-claustral founding (queens forage during nest foundation) and (iv) claustral founding (queens feed their first batch of workers by metabolizing their own nutritional reserves). The consequences of these nest founding modes described in literature are given in Table 2, along with the consequences of all co-occurring traits. The ecological back-ground to these consequences is further explained in Appendix 2. Ecological consequences of the nest founding modes and co-occurring traits were found to revolve around the time-window for initial colony founding, food availability during founding and dispersal limitations. The time-window for initial colony founding is strongly linked to site temperature as the time ant larvae need to develop increases greatly

Table 2. Traits and their consequences for survival used to build-up life-history strategies. Traits between brackets are strongly linked to the trait above. References to the main literature sources are given as footnotes.

Trait	Description	Consequence & preconditions for survival
Nest founding mode (Mature nest size) ^{1, 2} (Number of males and gynes) ^{1, 3} (Costs of producing a single gyne) ^{4, 5} (Mode of dispersal prior to nest foundation) ^{1, 2}	Nest splitting	Limited dispersal distance ^{1, 2}
	Social parasitism	Distribution limited to sites large enough for stable host populations ^{7, 8}
	Semi-claustral	High food availability needed during nest founding ⁹
	Claustral	Initial development time during nest founding restricted ¹⁰ causing high temperature dependence in species with slow larval development ^{11, 12}
Additional founding modes	Additional nest-splitting	Promotes expansion within already colonised sites ¹
	Pleometrosis	Speeds up initial development ^{13, 14}
Mode of colony growth (Colony age) ^{1, 2}	Independent	Long colony life-span ²
	Dependent	Short colony life-span ²
Development speed of worker-larvae	Fast	Short initial development time during colony founding ¹²
	Slow	Long initial development time during colony founding ^{12, 15}
Development stages capable of overwintering (Period of initial larval development) ⁶	Only adults	Determines time-window for colony founding
	Adults and larvae	
Timing of the nuptial flight	Early season	Determines time-window for colony founding
	Late season	
Period of initial egg-laying (Period of initial larval development) ^{1, 6}	Before winter	Determines time-window for colony founding
	After winter	

¹ Hölldobler and Wilson 1990; ² Seifert 2007; ³ Bourke 1999; ⁴ Keller and Passera 1989; ⁵ Stille 1996; ⁶ Kipyatkov 2001; ⁷ Holt et al. 1999; ⁸ Mabelis and Chardon 2006; ⁹ Johnson 2006; ¹⁰ Andrasfalvy 1961; ¹¹ Wagner et al. 1984; ¹² Kipyatkov 1993; ¹³ Waloff 1957; ¹⁴ Sommer and Hölldobler 1995; ¹⁵ Kipyatkov et al. 2004.

with decreasing temperature (Kipyatkov 1993; Kipyatkov et al. 2004; Wagner et al. 1984). This means that species with a narrow time-window for initial development are restricted to nest founding locations that are relatively warm, to ensure the completion of the development of the first worker batch before the onset of winter.

Based on the ecological consequences of the occurring trait combinations we arrived at four functionally different life-history strategies. All species with nest-splitting or parasitic founding as main nest founding mode are poor dispersers between sites and were therefore grouped to form strategy D (13 species). Due to the availability of workers during the nest founding phase they are much less affected by low food availabilities and low soil temperatures during nest founding. All semi-claustral and claustral species are reasonably good dispersers. The semi-claustral species are limited to sites with high food availability as their queens have to forage by themselves to feed their first batch of workers. They were grouped to form strategy F (11 species). The claustral species are not affected by the food availability during nest founding, as claustral queens feed their first worker batch from their own nutritional reserves. Some claustral species however, have a very narrow time-window for initial colony founding. The time available for development of the first batch of workers is determined by the species' phenology (timing of the nuptial flight and egg laying), its overwintering stages and its development speed. Time-constrained species are restricted to warm locations to complete development of the first worker batch before winter. All claustral species with a narrow time window were grouped to form strategy T (seven species). The fourth strategy, G (four species), consists of species which are all claustral, but with a broader time-window for initial development. These are more generalist species that are well adapted to cope with both low food availability and low temperature and are reasonably good dispersers.

Ant species richness

For strategies F and G the average number of species per pitfall trap series does not differ between sites (strategy F, $\chi^2 = 12.149$, $p = 0.205$, $df = 9$; strategy G, $\chi^2 = 15.038$, $p = 0.090$, $df = 9$; Figure 2). The number of species from strategy T, which need a high temperature during nest foundation before the onset of winter, does significantly differ between sites ($\chi^2 = 23.403$, $p = 0.005$, $df = 9$). This is also the case for the average number of species from strategy D, which are all limited in their colonization ability ($\chi^2 = 23.019$, $p = 0.005$, $df = 9$).

Site isolation

The degree of site isolation, defined as the distance between the study site and its next nearest chalk grassland, ranges from 0.1 to 3.0 km. The relation between this distance and the average number of species from strategy D per site is best described by an exponential regression (Figure 3). With increasing distance to the next nearest chalk grassland there is a significant exponential decline in the number of species from strategy D ($R^2 = 0.578$, $p = 0.011$, $df = 9$).

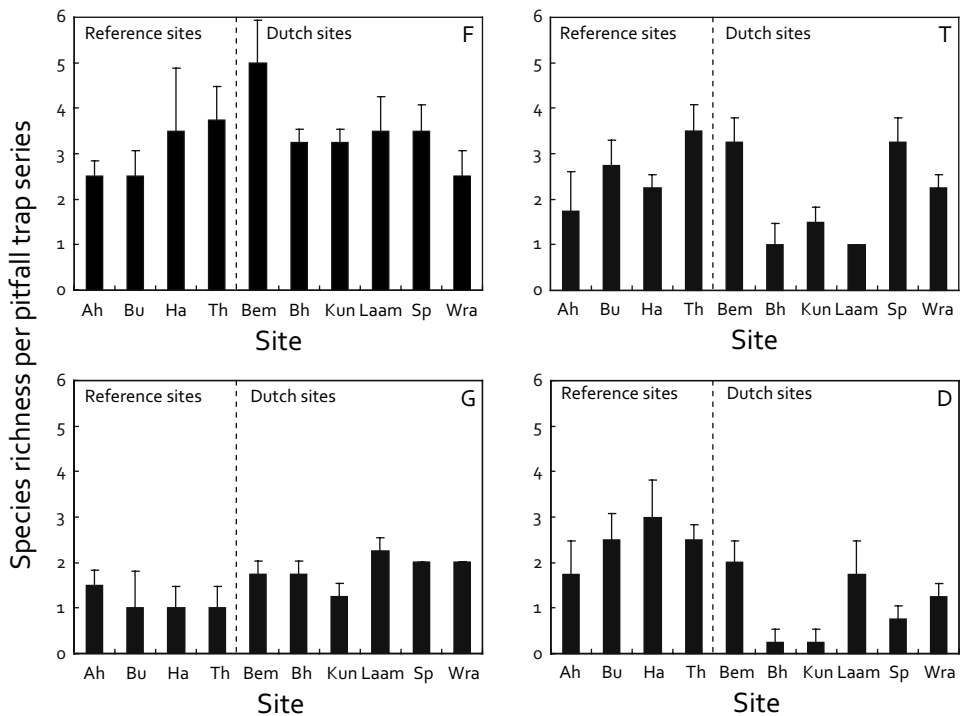


Figure 2. Mean number of species per pitfall trap series on each site (± 1.0 SE) for strategy F, T, G and D. Ah, Bu and Ha are German sites, Th is located in Belgium and Bem, Bh, Kun, Laam, SP and Wra are Dutch chalk grasslands.

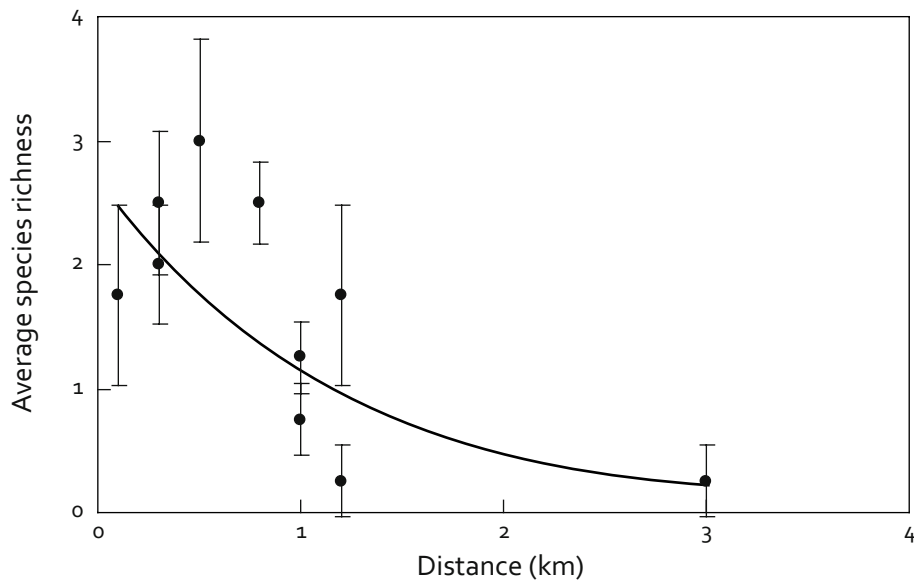


Figure 3. Relationship between the distance to the next nearest chalk grassland site and the mean number of species from strategy D per pitfall trap series on each site (± 1.0 SE). The significant exponential regression is plotted with the data ($R^2 = 0.578$, $p = 0.011$, $df = 9$).

Temperature

The relationships between the soil temperature on five warm days throughout the year and the number of species from strategy T per pitfall trap series are best described by linear regressions (Table 3). In summer and autumn (August 6, September 11 and November 8) there is a strong correlation between the soil temperature and the number of species from strategy T (Figure 4). In spring the correlation between the soil temperature and the number of species from strategy T is less pronounced (May 12) or not significant (24 June). Within each sampling location, soil temperatures throughout the season are strongly autocorrelated (Pearson correlation > 0.75, $p < 0.003$). There is however a significant effect of management timing on the changes in soil temperature during the summer season (ANOVA $F = 6.360$, $p = 0.024$, $df = 15$; Figure 5). Sites that are managed in summer are significantly warmer in August than sites that are only grazed or mown in winter (ANOVA $F = 17.342$, $p < 0.001$, $df = 22$), while there is no difference in soil temperature between these sites in May (ANOVA $F = 2.069$, $p = 0.168$, $df = 18$).

Table 3. Linear regression results for the relationship between the average daily temperature on five warm days and the number of species from strategy T.

Date	R ²	p	df
May 12 2008	0.265	0.024	19
June 24 2008	0.167	0.066	21
August 6 2008	0.464	0.001	23
September 11 2008	0.335	0.009	19
November 8 2008	0.381	0.008	17

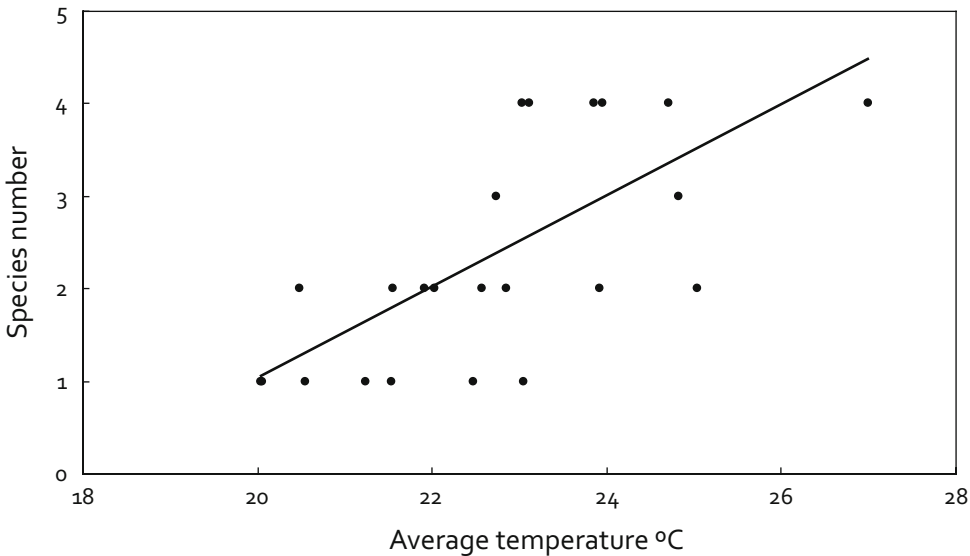


Figure 4. Relation between the average soil temperature on a warm day in August (August 6 2008) and the number of species from strategy T per pitfall trap series. The significant linear regression is plotted with the data ($R^2 = 0.464$, $p < 0.001$, $df = 23$).

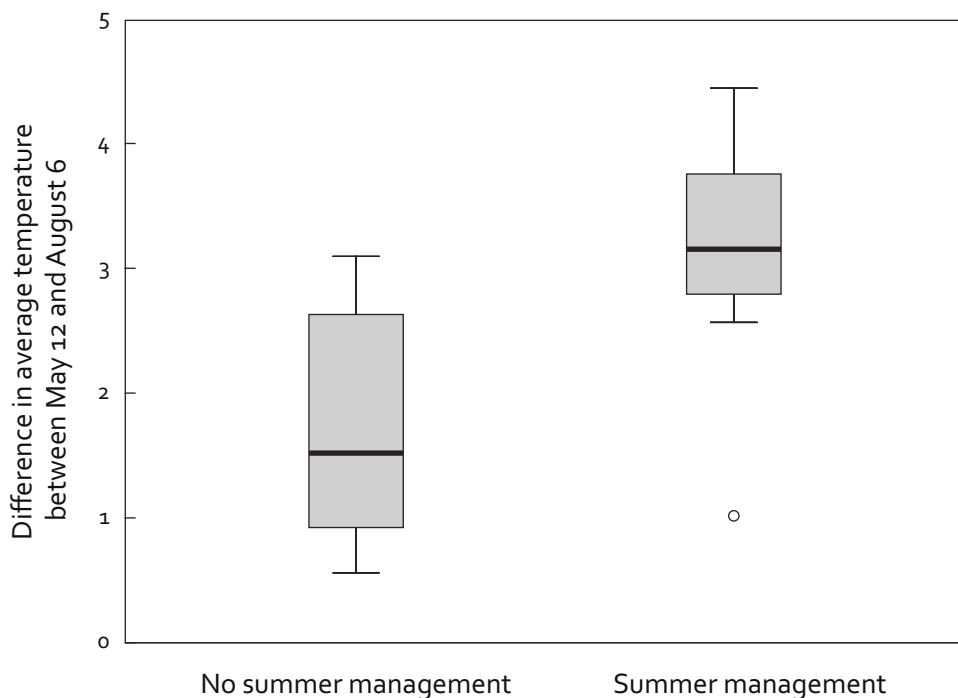


Figure 5. Boxplot showing the significant difference (ANOVA $F = 6.360$, $p = 0.024$, $df = 15$) in the change in soil temperature between May 12 and August 6 2008 between sites with and without summer management.

Discussion

By grouping species according to the ecological consequences of their reproduction, development, synchronization and dispersal traits we could assign the 35 ant species found in our study sites to four functionally different life-history strategies. We identified three main variables which will differently affect ants with different life-history strategies; the degree of isolation of their habitat, the temperature during nest founding before the onset of winter and the food availability during nest founding. Tests of these theoretically predicted responses matched field observations, as indeed time constrained species strongly responded to summer soil temperature, whereas dispersal limited species showed a strong relationship with site isolation. While food availability and habitat isolation in relation to a species' dispersal capability are of obvious importance, low temperature has also previously been identified as one of the most critical stress factors for ant communities (Andersen 1995).

Bottlenecks for ants in Dutch chalk grasslands

The aim of our study was to use the mechanistic understanding of species-environment relationships to formulate management recommendations to improve the status of the ant fauna in the study sites. From the complex web of environmental factors affecting

the study sites (site size, habitat isolation, aspect, inclination, current management, management history, eutrophication and past abandonment) we have identified two main issues affecting the ant fauna; the degree of habitat isolation and the soil temperature in summer. Both of these issues are connected to different types of management efforts.

Habitat isolation

Our results show that the number of ant species from strategy D decreases exponentially with increasing distance to the next nearest chalk grassland. This implies that at more isolated sites species from strategy D cannot reach these sites once they have disappeared. Whether ant species will actually disappear from a site is related to habitat quality (Dauber et al. 2005; 2006). It is likely that in some or most Dutch sites past degradation has caused local extinctions, while in other sites the habitat quality has always been suitable for these species. Incorporating detailed data on the site history would therefore shed more light on the exact relation between site isolation and recolonization probabilities. It is clear however, that at sites which are more than one kilometre apart from their next nearest chalk grassland, and especially at sites as isolated as Kunderberg, species from strategy D are severely threatened. So far, studies on the effects of isolation and fragmentation on ants in temperate grasslands have mainly focused on fragment size rather than isolation itself (Dauber et al. 2006), although site isolation has previously been suggested to be of importance (Mabelis and Verboom 2009). Our results show that management actions aimed at counteracting habitat isolation are of prime importance for the conservation of ant communities in these sites. For species from strategy D small steppingstones in the landscape are insufficient (see Appendix 2). The most effective management actions are to optimize and enlarge existing chalk grassland sites in order to promote species persistence and to create new nutrient-poor grasslands in close proximity to existing sites.

Summer soil temperature

We successfully tested the prediction that the soil temperature especially in summer and autumn is of great importance to the time-constrained species from strategy T. The soil temperature in chalk grasslands is affected by the aspect and the inclination of the site and by the vegetation structure, higher and denser swards being much cooler than short swards (Stoutjesdijk and Barkman 1987). Sward height itself is strongly related to the management regime. Accordingly, we demonstrated an effect of management timing on soil temperature, with higher summer soil temperatures in sites that are mown or grazed in summer compared to sites that are only managed in autumn or winter. This temperature difference of about 2° C in average daily temperature on a warm day is likely to indeed cause a significantly longer development time for worker larvae (Andrasfalvy 1961; Kipyatkov 1993; Kipyatkov et al. 2004). Species from strategy T can thus only occupy sites with a suitable aspect and inclination, if the management intensity and timing are sufficient to create an open sward with a sufficiently high soil temperature in summer. It seems that with the present increased nutrient levels in the Dutch chalk grasslands (Smits 2010) management efforts that are restricted to autumn or winter are insufficient to produce such an open sward, causing the decline in species from strategy T. Previous studies have already shown that ant communities are strongly influenced by sun exposure (Dauber et al. 2005, 2006). Our study demonstrates that specifically the soil temperature in summer, during the period of nest founding before the onset of winter, is a key factor.

This is crucial added information for formulating management measures. We would recommend site managers of chalk grasslands with increased nutrient levels to shift the main management period to the summer season (May-June), where necessary combined with low intensity autumn grazing. This is most likely also beneficial for the chalk grassland vegetation (Smits 2010) as more nutrients are removed in this period. Summer mowing or grazing may however create new problems like insufficient nectar plants availability for butterflies and bees. Therefore, sites should be divided into several compartments which are managed separately, with ample time between compartments to allow regrowth and reflowering of food plants. Such compartmentation also allows to tailor the management intensity to the local situation. In this way the negative effects of disturbance caused by management actions can be minimised, while optimising the vegetation structure. The management regime we propose here has already been applied successfully for several years in a number of chalk grasslands in the Viroin region (Belgium), which also tend to be inhabited by higher numbers of characteristic ant species (Dekoninck et al. 2006). This is however no guarantee for success as the nitrogen accumulation in the soil and the landscape configuration differ dramatically from the Dutch sites. Field testing of the proposed management alterations is essential to really improve management for chalk grassland ants.

Life-history strategies as a tool

The use of life-history traits to analyse species responses to their environment is growing rapidly (e.g. Bremner et al. 2006; Cristofoli et al. 2010; Lambeets et al. 2009). However, only a limited number of studies have incorporated interactions between traits, using aggregated traits (Öckinger et al. 2010) or life-history strategies (Siepel, 1995; Van Turnhout et al. 2012; Verberk et al. 2008a, 2008b). One reason to use traits rather than strategies is that the compilation of meaningful life-history strategies is a very time consuming process. In addition, the compilation of strategies is often termed somewhat arbitrary, even though it is based on logic (Verberk 2010). From an ecological perspective however, one could argue that ignoring the interactions between traits completely or weighing all traits equally, as is done in multivariate statistical analyses (clustering, ordination), is equally arbitrary if not more so. Within species, traits are not independent, they are linked to form an integrated response to particular ecological problems (Siepel 1994; Siepel 1995; Stearns 1976). The interactions among life-history traits can be essential to understand species responses to their environment (Davies et al. 2004). Our case study illustrates this. Single traits like the timing of the nuptial flight, the period of initial egg-laying, the development stages capable of overwintering and the development speed of worker larvae did not show clear ecological consequences. Only when taken together, it becomes clear that the time-window for initial colony founding differs between species, causing some species to be restricted to warm habitats.

The explicit incorporation of trait interactions and the deduction of ecological consequences by way of logical reasoning are the main advantage of the life-history strategy approach. It gives insight into the mechanisms underlying species-environment relationships, providing clear testable hypotheses (see also Verberk et al. 2010b). This increases our understanding regarding which conditions are most important for the species group under study. Our case study, for example, revealed that specifically soil

temperature in summer and early autumn is an important parameter for ants in chalk grasslands, rather than soil temperature in general. This led to the specific hypothesis that summer management is essential, which is confirmed by our field data. Multivariate top-down approaches and single-trait approaches would likely have overlooked this factor. Without the specific ecological knowledge derived from the combinations of life-history traits, researchers would have measured soil temperature with no specific timing, likely missing the effect of summer management. In addition, the life-history strategy approach enabled us to pinpoint the main factors shaping the ant species composition even though the study sites differed with respect to a large number of environmental factors. Strategies can be represented by different species in different sites making it possible to compare sites with different local species pools, for example located in different geographical regions. The use of life-history strategies also decreases the biasing effects of stochastic extinction and colonization patterns for single species, which for example, severely hamper the usefulness of single indicator species (Andelman and Fagan 2000). The mechanistic character of our approach is an essential difference to the earlier classifications of ants by Andersen (1995) based on functional groups, taxonomy and habitat requirements (generalist/specialist).

Conclusion

The life-history strategy approach is a valuable tool to get insight in the factors shaping the local species composition. It is especially valuable to disentangle and ascertain the importance of factors related to either local habitat suitability or regional connectivity (Verberk et al. 2010b). Life-history strategies function as indicators for specific ecological processes, focusing on those processes that are most important to the species group under study. The general method, here demonstrated on ants in chalk grasslands, can be used for all organisms and ecosystems. The life-history strategy approach is a valuable alternative to the use of single indicator species and to top-down approaches that try to identify key factors by analysing the variation in environmental parameters. The most important advantage of this method is that it provides understanding of the underlying mechanisms. In effect, it compares processes rather than the occurrence of single species. These features make this method especially suitable to translate species-environment relationships into practical management measures.

Acknowledgments

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Appendix 1. Life-history traits

Table A1. (see right page) Ant species captured and their main traits per life-history strategy (S). The main literature source for each trait is given in every column head, additional sources are given in footnotes. The founding mode is semi-claustral (s-c), claustral (cl), independent claustral or semi-claustral (ind), by nest-splitting (ns) or parasitic (p). In addition founding can be haplometrotic (h) or facultatively pleometrotic (fpl). The colony growth mode is independent (ind) if own workers are produced or parasitic (p) if queens rely on host-workers throughout their life-cycle. The column 'Development speed' depicts the intrinsic speed of larval development. The period of the nuptial flight is given in 0.5 month intervals from April to October where white periods show main swarming periods and grey periods depict that some swarming events may occur. Larval diapause stage lists which larval stages are capable of overwintering. In the column 'first egg laying' '?' indicates that no specific information was found, but that the given 1st egg-laying period for newly mated queens is assumed based on the period of the nuptial flight.

¹ All non-parasitic *Myrmica* species exhibit semi-claustral colony founding and nest-splitting (Seifert 2007)

² Kutter 1977 and Dumpert 1978 in Keller and Passera 1989

³ P. Boer personal observation

⁴ Schoeters and Vankerhoven 2001

⁵ Stitz 1939

⁶ Eidmann 1943

⁷ Unpublished data of first and second authors suggest queen foraging after diapause

⁸ Andrasfalvy 1961

S	Trait Source	Founding mode Seifert 2007	Growth mode Seifert 2007	Development speed Kipyatkov 1993	Nuptial flight period Seifert 2007; Boer 2010	Larval diapause stage Kipyatkov 1993; 2001	1 st egg laying Seifert, 2007
F	<i>Myrmecina graninicola</i>	s-c	independent	slow	A A S S	unknown stage ⁶	after diapause ⁷
F	<i>Myrmica lobicornis</i>	s-c	independent	slow	J A A S	last	after diapause ⁷
F	<i>Myrmica rubra</i>	s-c, ns	independent	slow	A S	last	after diapause ⁷
F	<i>Myrmica ruginodis</i>	s-c, ns	independent	slow	J J A A	last	after diapause ⁷
F	<i>Myrmica sabuleti</i>	s-c ¹ , ns ⁴	independent	slow	J J A A S	last	after diapause ⁷
F	<i>Myrmica schencki</i>	s-c	independent	slow	J A A S S	last	after diapause ⁷
F	<i>Myrmica scabrinodis</i>	s-c, ns	independent	slow	A A S	last	after diapause ⁷
F	<i>Myrmica speciosides</i>	s-c	independent	slow	J J A A S	last	after diapause ⁷
F	<i>Ponera coarctata</i>	s-c, fpl	independent	slow	A A S S	none	after diapause ⁷
F	<i>Stenamma debile</i>	s-c, ns, fpl	independent	slow	S S O O	last	after diapause ⁷
F	<i>Tennothorax interruptus</i>	s-c	independent	slow	J J J A A	unknown+egg	after diapause ⁷
T	<i>Lasius (Lasius) alienus</i>	cl ₂ , fpl ¹	independent	slow	J J A A S	all	directly ^a
T	<i>Solenopsis fugax</i>	cl, ns, h	independent	slow	S S	unknown stage ⁶	after diapause ⁸
T	<i>Tetramorium caespitum</i>	cl, h ³	independent	slow	J J J J	last	directly [?]
T	<i>Tetramorium impurum</i>	cl, h ³	independent	slow	A A S O O	last	after diapause [?]
T	<i>Formica (Serviformica) cunicularia</i>	cl, ns, fpl	independent	fast	J J J J	none	directly [?]
T	<i>Formica (Serviformica) lusatica</i>	cl, ns, fpl	independent	fast	J J J J	none	directly [?]
T	<i>Formica (Serviformica) rufibarbis</i>	cl, ns, fpl	independent	fast	J J J J	none	directly [?]
G	<i>Formica (Serviformica) fusca</i>	cl, ns, fpl	independent	fast	J J J A A S	none	after diapause
G	<i>Lasius (Cautolaius) flavus</i>	cl ² , fpl	independent	slow	J J A A	all	directly & after diapause
G	<i>Lasius (Lasius) niger</i>	cl ¹ , fpl	independent	slow	J J A A	all	directly & after diapause
G	<i>Lasius (Lasius) platythorax</i>	cl ¹ , fpl	independent	slow	J J J A A	all	after diapause ¹
D	<i>Anergates atratulus</i>	p	parasitic	?	M M J J J A A	last ⁵	directly
D	<i>Myrmica karavajevi</i>	p	parasitic	slow	J J A A	last	directly [?]
D	<i>Lasius (Chthonolasius) fuliginosus</i>	p, fpl	independent	slow	J J J J A A S	all	directly
D	<i>Lasius (Chthonolasius) jensi</i>	p	independent	slow	J J A A S	all	directly
D	<i>Lasius (Chthonolasius) meridionalis</i>	p, fpl	independent	slow	J J A A S O	all	directly
D	<i>Lasius (Chthonolasius) mixtus</i>	p, fpl	independent	slow	J A A S O	all	after diapause
D	<i>Lasius (Chthonolasius) subularum</i>	p	independent	slow	A S O	all	directly & after diapause
D	<i>Lasius (Chthonolasius) umbratus</i>	p, fpl	independent	slow	J J J A A S S	all	directly
D	<i>Lasius (Dendrolasius) distinguendus</i>	p	independent	slow	J J J A A	all	directly [?]
D	<i>Formica (Formica) polycetena</i>	ns, p	independent	fast	A M M J	none	directly
D	<i>Formica (Formica) pratensis</i>	ns, p	independent	fast	A M M J J J J	none	directly
D	<i>Formica (Raptiformica) sanguinea</i>	ns, p	independent	fast	J J J J A A	none	directly
D	<i>Tapinoma erraticum</i>	ns, ind ⁵	independent	?	J	first	directly

Appendix 2. Theoretical back-ground to the ecological consequences of occurring trait combinations

Claustral and semi-claustral (independent) founding

Both claustral and semi-claustral queens feed the first batch of worker larvae by themselves. During the nest founding phase they have no workers to collect food and no large nest with improved microclimatic conditions. In claustral queens the amount of food available for raising the first batch of workers is predetermined at the moment the queens start nest foundation, while in semi-claustral queens food is gathered throughout the nest founding stage. This enables semi-claustral queens to produce more and bigger workers when food is prevalent, but also causes brood failure when food is too scarce (Johnson 2006). Claustral species are not limited by the food availability during founding, but in these species the founding phase is limited in time, as queens will not be able to survive more than one winter on their nutritional reserves (Andrasfalvy 1961). Claustral species thus need to have workers by the end of the second summer to take up foraging tasks, while semi-claustral species are not affected by this time-constraint. The time window for larval development is further determined by whether species start laying eggs directly after their nuptial flight or postpone egg-laying until spring. The development time of ant larvae is strongly temperature dependent (Kipyatkov et al 2004; Wagner et al. 1984). Therefore, the time window, combined with the rate of larval development and the larval instar capable of overwintering determines to what extent species are constrained to warm nest sites. Claustral and Semi-claustral species which start laying eggs directly after their nuptial flight are restricted to warm nest sites if they have late nuptial flights, slow larval development or larvae that can only overwinter in late instar stages. Claustral species whose queens overwinter once before they start laying eggs are also restricted to warm nest sites if they have slow larval development, as they need to have adult workers within one season. The speed of larval development depends in the first place on intrinsic factors. The duration of ontogenesis from egg to pupa is much shorter for *Formica* species (20-25 days at 25°C) than for *Myrmica* (e.g. *Myrmica rubra* 35 days at 25°C) (Kipyatkov 1993) or *Lasius* species (e.g. *Lasius niger* 40 days at 25°C) (Kipyatkov et al. 2004). In addition, the speed of development in the founding phase can be enhanced by the presence of several founding queens (Sommer and Hölldobler 1995; Waloff 1957). Based on the timing of the first egg-laying period, the timing of the nuptial flight, the larval instar capable of overwintering and the speed of larval development, the claustrally founding ant species in this study could be divided into time-constrained (and thus temperature dependent) and non-time-constrained species. The time-window was defined as constrained if i) species have one season for complete development from egg to adult and have a low intrinsic development speed and no additional traits that speed up development (e.g. pleometrosis or availability of workers), ii) species have a high intrinsic development speed, but only half a season (nuptial flight no earlier than June) for complete development from egg to adult or iii) species have a low intrinsic larval development speed and only half a season for development from egg to last instar larva or an even shorter period for development from egg to first instar larva. By these definitions, a limited time-window and consequent high temperature dependence only occurred in the claustrally founding species in our study, not in semi-claustral species.

Nest-splitting

Nest-splitting is an effective way to avoid the workerless phase. It provides a queen from the start with an extensive worker force for nest building and food collection. However, in nest-splitting species new nests can only be established close to the old nest, since the whole group of workers and queen(s) needs to reach the new nest site on foot. Although this enhances local population expansion (Hölldobler and Wilson 1990), it also severely limits the dispersal capabilities of these species between sites (Hölldobler and Wilson 1990; Seifert 2007). All mainly nest-splitting species in this study also have an alternative nest founding mode for dispersal over longer distances. *Tapinoma* species can additionally found nests independently and all mainly nest-splitting *Formica* species additionally

found nests by social parasitism. As only a small proportion of all nests is founded through these additional strategies, long distance dispersal is still limited, making these species especially prone to local extinction following isolation.

Social parasitism

Nest founding through social parasitism is also an effective way to avoid the workerless phase, supplying the queen not only with an extensive worker force, but also with an existing nest with thermoregulation capacities. Parasitic nest founding does not in itself restrict the dispersal capabilities of ant species, but it does limit their distribution. Parasitic species can only inhabit sites with a sufficiently large and stable host population (Holt et al. 1999). Therefore, they are more prone to local extinction (Cronin 2004) and they cannot use isolated host populations in a landscape as steppingstones from which they could more easily reach suitable habitats (Mabelis 1994; Mabelis and Chardon 2006; Mabelis and Korczyńska 2001). This means that parasitic species will be more susceptible to effects of isolation than independently founding species. This effect will be most pronounced in the permanently parasitic species which do not produce own workers and thus need a steady supply of new host colonies, given the limited life-span of host workers (Seifert 2007). Colonies of temporarily parasitic species can live-on independently for a substantial period enabling them to survive in sites with a smaller host population or even to overcome a short period of host absence. This is especially true for the temporarily parasitic species that also exhibit nest-splitting as they have an alternative strategy to reproduce locally. However, these species are more limited in their colonization capacity because only a small fraction of the reproductive effort is invested in long-distance nest founding by individual queens.



Mergelland sheep grazing on Kunderberg (Photo: Toos van Noordwijk)

Chapter 4

Effects of large herbivores on grassland arthropod diversity

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**C.G.E. van Noordwijk and F. van der Plas provided a substantial and equal contribution to this chapter.*

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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 140 studies on this topic of which 24 simultaneously investigated plant and arthropod diversity. Using the data from these 24 studies, we compared the response 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 to consider the specific requirements of arthropods when applying grazing management and to include arthropods in monitoring schemes. Conservation strategies aiming at maximizing 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.

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 11,000 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 (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 (Ostermann 1998; WallisDeVries 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 et al. 1988; Olff and Ritchie, 1998). Reported effects on arthropod diversity are equally diverse, with studies reporting negative (e.g. Kruess and Tscharntke 2002a, 2002b; Pöyry et al. 2004), positive (Woodcock and Pywell 2010; Joern 2005), or neutral (Bestelmeyer and Wiens 2001; Hofmann and Mason 2006) effects of large herbivores. Intuitively, a strong positive relation 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 (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 (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 synthesize 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 and Wardle (2003)), play a role in forested landscapes (included in the review by Suominen and 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 et al. (2012) and Joern and 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 synthesized by Tschardt 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 between 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, hay cutting or abandonment. Only studies meeting the following three criteria were assessed: 1) Published or in press in international, peer-reviewed scientific journals in ISI 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 Appendix 1) in combination with “graz*” in ISI Web of Science.

Dataset description

Our search yielded 140 studies assessing the effects of large herbivores on arthropod communities published between 1940 and May 2013, sometimes in combination with other management types (Appendix 1). An overview of the taxonomic and geographic focus of all 140 studies is given in Figure 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 (Figure 1a). More than half of the studies assessed only one taxonomic group, with less than 25% of studies assessing more than two arthropod taxa (Figure 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 data was collected for eight years or more (Figure 1c).

The majority of grazing studies were conducted in Europe (>65%; Figure 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 (Appendix 2). The vast majority of studies was published after the year 2000 (Figure 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 et al. 2005; Gómez and González-Megías 2007). The controlled experiments usually ran less than ten years (although some impressive examples of long-term experimental grazing research exist, see Appendix 1) and generally had a relatively small number of replicates (max. three). In the historical studies, effects of grazing were compared among a number of sites that historically differed in densities or species of herbivore (e.g. Smith 1940; Kruess and Tschardt 2002a, 2002b; Nickel and 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.

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 140 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

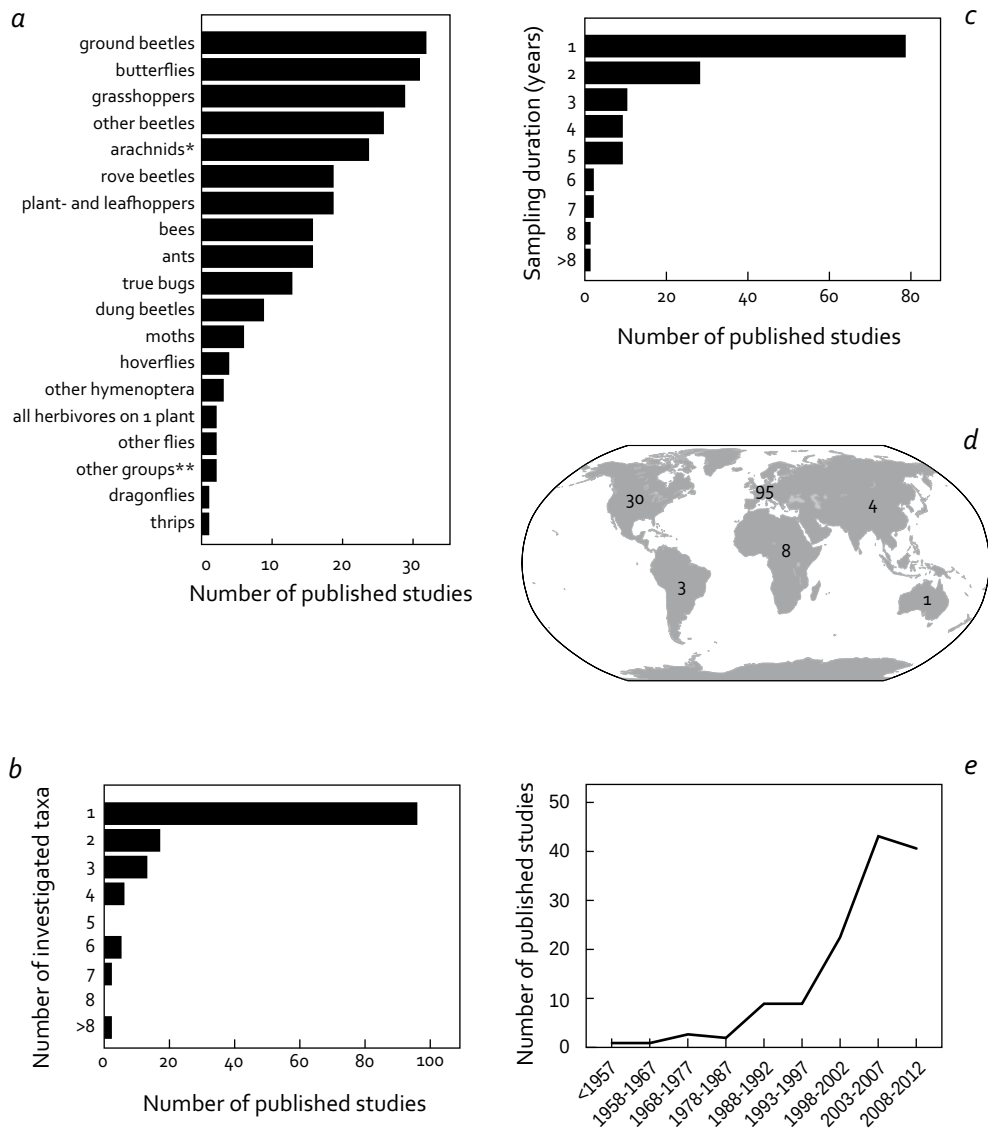


Figure 1. Research focus of the 140 published studies assessing effects of large herbivores on arthropod diversity, conducted in open landscapes (grass- or heathlands), with arthropods identified to species level: a) studied taxa, b) taxonomic spread (number of investigated taxa), c) duration of sampling, d) geographic location, and e) year of publication. We documented the identity of the most commonly assessed taxonomic groups (usually to order level, but sometimes to family or class level, see Appendix 3). A complete list of the analysed studies and definitions of arthropod groups can be found in Appendix 1. *Arachnids: spiders, harvestmen, pseudoscorpions; **Other groups: Mantodea, Phasmatodea, Neuroptera, Dermaptera etc.

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 directly obtained 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 response variable, we used untransformed response ratios of the change in richness with an increase in grazing intensity ($(r_2 - r_1)/r_1$ 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 et al. 1999; see also Milchunas and 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 the Appendix 1 and 3.

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 random factors. Secondly, we analysed which variables explained the response of arthropod diversity to an increase in grazing intensity. For this analysis we used the 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 vs. moderate density, whereas ‘3’ indicates a large difference in density e.g. ungrazed vs. 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 get 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 Development 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 (Figure 2a). Across all studies, arthropod diversity responded significantly negatively to an increase in grazing intensity (GLMM: $\mu = -0.14 \pm 0.04$, $t = -3.36$, $p = 0.002$, Figure 2b), 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 (Figure 2b). When the two effects were compared, the response of arthropod diversity was significantly more negative than that of plant diversity (GLMM: $\mu = -0.15 \pm 0.03$, $t = 4.54$, $p < 0.001$, Figure 2a). The second mixed model, including multiple explanatory variables, revealed a significant, but weak positive relation between the responses of plant and arthropod diversity to grazing ($\beta = 0.41 \pm 0.13$, $t = 3.28$, $p = 0.004$, model fit: $\chi^2 = 9.65$, $p = 0.002$ Figure 2b), with a negative intercept ($\mu = -0.15 \pm 0.04$). We found no significant effect of ecosystem productivity ($\chi^2 = 1.21$, $p = 0.55$), study duration ($\chi^2 = 6.98$, $p = 0.14$), experimental type ($\chi^2 = 0.56$, $p = 0.45$), or difference in grazing intensity ($\chi^2 = 3.94$, $p = 0.27$). 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

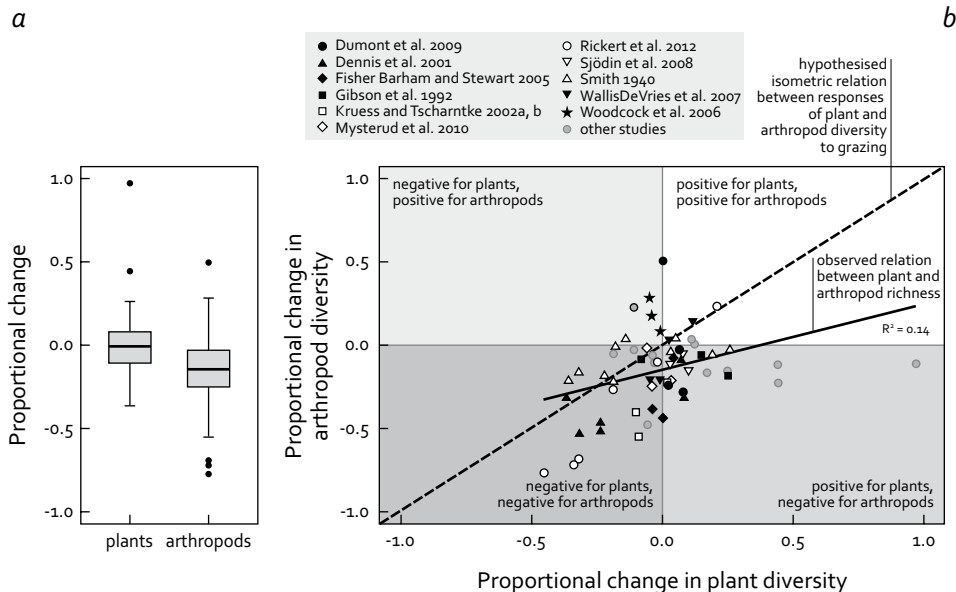


Figure 2. Comparison of the response of plant and arthropod diversity to an increase in grazing intensity, significant according to glmm (a), and the significant relationship between these responses (b) according to glmm. Data were extracted from 24 studies published between 1940 and 2013 reporting on the effects of grazing on both plant and arthropod diversity, supplemented with data obtained from several authors (see Appendix 1).

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

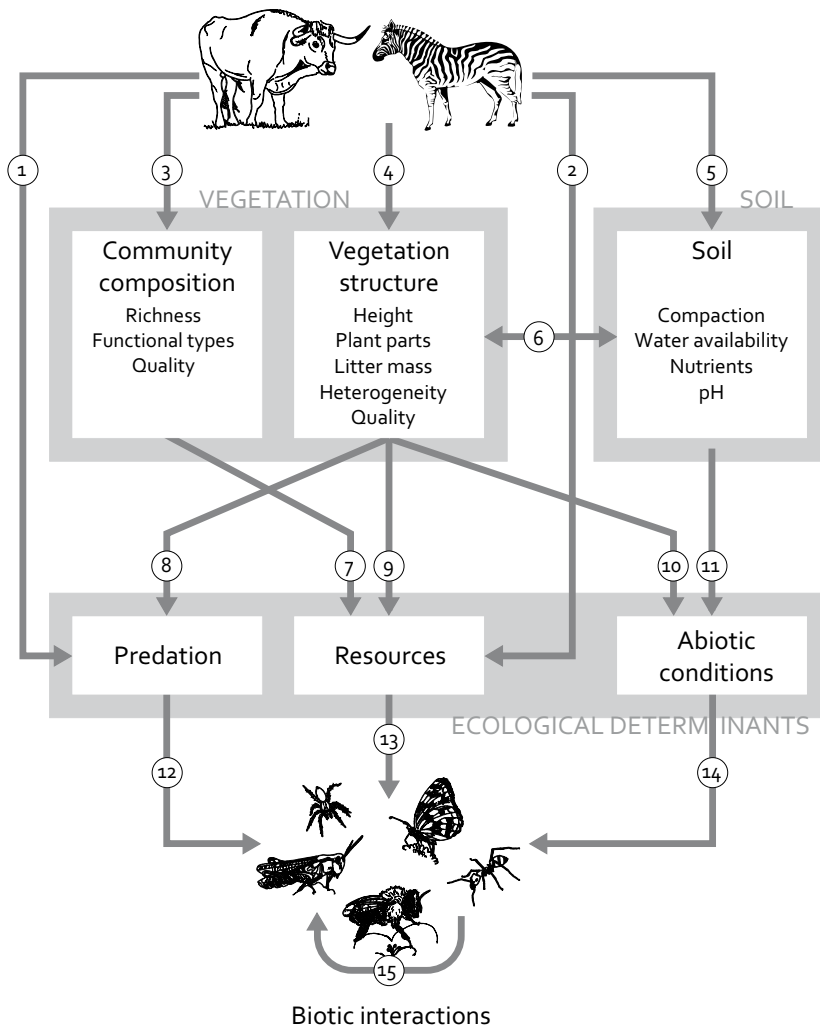
The quantitative analysis in the previous section showed that 1) the prevailing effect of large herbivore grazing on arthropod diversity is negative, 2) within studies, arthropod diversity responds more negatively to grazing than plant diversity, 3) the response of plant diversity to grazing is a poor 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 (Dauber et al. 2005; Oertli et al. 2005).

In order to understand these patterns, we will focus on the potential mechanisms by which large herbivores affect arthropod species. Figure 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 (Figure 3, path1), but also by supplying resources for specialized groups such as dung feeders and scavengers (Figure 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 and González-Megías 2007; Bonal and Munoz 2007; chapter 5). The potential consequences at the community level have rarely been measured, but defoliation by mowing is known to cause high direct arthropod mortality (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



Path 1: direct effects: trampling and unintentional predation. **Path 2:** direct effects: dung, carcasses, blood, live tissue. **Path 3:** Increase or decrease in plant species richness and changes in functional groups, the direction of which depends on their density and the properties of the ecosystem. **Path 4:** changes in vegetation structure: lowering of vegetation height through defoliation and changes in horizontal heterogeneity resulting from selectivity. **Path 5:** Changes in soil conditions (pH, bulk density). **Path 6:** Changes in soil conditions can affect vegetation characteristics. **Path 7:** A change in plant species richness can affect species richness of associated insect herbivores. **Path 8:** A reduction in vegetation height can increase predation risk by vertebrate predators. **Path 9:** Direct competition for resources between the base of the arthropod food web and large grazers. **Path 10:** A reduction of vegetation height increases surface temperatures, but decreases shelter from climatic extremes and essential structures for egg deposition or web construction. **Path 11:** changing soil properties may affect insects that spend part of their lives underground. **Path 12, 13, 14:** the combined changes in abiotic conditions, resources and predation determine the effects on each arthropod species, and will therefore affect arthropod populations and communities. **Path 15:** due to the interactions between arthropod species, changes in species' abundances might have cascading effects on other species, with ultimate effects on total species richness.

Figure 3. A conceptual framework of mechanistic pathways by which large herbivores directly and indirectly affect arthropod diversity. Arrows represent mechanisms, with numbers referring to the accompanying list and the main text. The upper row of boxes represents biotic and abiotic conditions that are modified by large herbivores; the lower row of boxes represents the mechanisms operating on arthropod individuals, populations and communities.

(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 (chapter 5). These differences in the vulnerability to incidental ingestion between 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 and Cumming 2003; Hobbs 2006, Figure 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 and Maes 2008; Woodcock and Pywell 2010) 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 below). 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 (Figure 3, path 1). Additionally, frequent disturbance by large herbivores may decrease habitat suitability for arthropods. This may again be of extra importance for less mobile species – like many larval insects – that could experience difficulties in returning to their host plants (Dennis et al. 1998; Kruess and Tscharrntke 2002a), and may even be evident at low herbivore density, when no measurable effect on vegetation characteristics is documented (Kruess and Tscharrntke 2002b).

Conversely, large herbivores may have positive effects by directly supplying resources to arthropods in the form of dung, carcasses, blood and living tissue (Figure 3, path 2). Studies investigating the effect of dung on arthropod communities mostly focused on dung beetles, despite the fact that also termites (Freyman et al. 2008) and various fly families 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 decomposition rates (Wall and Strong 1987; Beynon et al. 2012).

Although it is obvious 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 (Figure 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). For arthropods, short and tall vegetation types provide different abiotic conditions, food resources and predation risk (Figure 3, path 8, 9, 10). The currently emerging insights how these differences affect arthropod diversity will be outlined below.

The abiotic conditions arthropods are exposed to, differ vastly between short and tall vegetation (Figure 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 (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 (Figure 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 specialized herbivorous insects depend upon (Thomas et al. 1986; Van Klink et al. 2013), 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 (Figure 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 and Pywell 2010). Consequently, arthropod diversity has often been found to decrease with increasing densities of large herbivores (Dennis et al. 1997; Kruess and Tscharrntke 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 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, defecation 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 et al. 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 vegetation 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 and Young 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 (Kruess and Tschardt 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 (Figure 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. 2013). 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 hypothesized 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 Tschardt 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 its 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 Tschardt 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; Tschardt 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 (Figure 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) (Figure 3, path 5). Changes in soil conditions can lead to changes in plant communities (Liddle 1997) (Figure 3 path 6), but can potentially also have direct effects on aboveground arthropods (Figure 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 between arthropod species

Like all organisms, co-occurring arthropod species interact in myriad ways, including resource competition, predation and mutualistic interactions (Figure 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 (Tscharncke 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. 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 (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 Tscharncke 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 a 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 (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 between 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 (Figure 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. 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. 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 Tscharrntke 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 and Ritchie 1998), creating opportunities for a wider group of specialist herbivores. Also for species such as dung beetles and parasites resource abundance will increase with grazing.

Large herbivores often strongly modify the abiotic environment experienced by arthropods. 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. 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.

High densities of large herbivores are likely to be always detrimental to arthropod diversity, although some arthropod species or groups may profit. This is indeed supported by most empirical studies (Gibson et al. 1992a; Kruess and Tscharrntke 2002a, 2002b; Nickel and Hildebrandt 2003; Rickert et al. 2012). Studies reporting otherwise (Vulliamy et al. 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 colonization by new species (Olff and Ritchie 1998). Since there is no evidence for an important role of competition in limiting arthropod diversity, 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). Especially immature stages have been found to 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, 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 synchronized (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; chapter 3).

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 (Ostermann 1998; WallisDeVries 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 (Figure 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. 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. 2010b, 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, 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 et al. 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 Tschardtke 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 (Tschardtke 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 (chapter 3), but can also be used to actively suppress populations of pest species (Onsager 2000).

Next steps

From this review, clear mechanisms explaining the patterns of arthropod diversity in grazed ecosystems have emerged. Analysing the combined effects of these mechanisms 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 (to what extent are diversity and composition 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 to consider the specific requirements of arthropods and to include 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.
- 6) Conservation strategies aiming at maximizing 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.

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Appendix 1. Used studies

Table A1. List of 140 published studies assessing the impact of grazing on arthropod diversity. Taxonomic groups are based on the definitions found in publications. In some cases insects from all orders were identified, but not all taxa were necessarily assessed using appropriate trapping methods. Here we excluded taxa that were not adequately sampled, even if one or several species of this group were reported (see for example Smith 1940 and Zhu 2012, where ground dwelling beetles were sampled using sweep nets). Several small orders (such as Mantodea (praying mantes), Phasmatodea (stick insects) and Neuroptera (lacewings)) were in these cases reported with low numbers of species. Here, we pooled these orders under "other groups". Type of study: "exp": experimental manipulation of grazer densities; "hist": surveyed sites with different grazing histories.

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
Andresen et al. (1990)	Germany	coastal salt marsh	ground beetles, spiders	exp.	0 / 0.5 / 1 / 2 cattle ha ⁻¹	4 yr	1 yr	
Azcaráte and Peco (2012)	Spain	mediterranean grassland	ants	hist.	grazed / ungrazed	1 yr	n/a	
Báldi et al. (2013)	Hungary	semi-natural grassland	beetles, bees, leafhoppers, true bugs, grasshoppers, spiders	hist.	intensive / extensive	1 yr	n/a	y
Balmer and Erhardt (2000)	Switzerland	calcareous grassland	butterflies	hist.	0-30 years after abandonment	1 yr	0-30	
Batáry et al. (2007a)	Hungary	steppe	beetles	hist.	intensive / extensive	1 yr	>5	
Batáry et al. (2007b)	Hungary	plains	grasshoppers	hist.	intensive / extensive	1 yr	n/a	
Batáry et al. (2010)	Hungary	steppe, grassland	bees	hist.	intensive / extensive	1 yr	n/a	y
Bates et al. (2007)	United Kingdom	exposed riverine sediments	beetles	hist.	gradient of grazing intensity	1 yr	n/a	
Bestelmeyer and Wiens (2001)	United States	semi-arid rangeland	ants	hist.	grazed / ungrazed	1 yr	n/a	
Blake et al. (1994)	United Kingdom	woodland, moorland, grassland	ground beetles	hist.	gradient of grazing intensity	7 yr	n/a	
Blight et al. (2011)	France	pseudo-steppe	beetles	exp.	grazed / ungrazed	1 yr	4 yr	
Bock et al. (2007)	United States	urban grassland	butterflies	hist.	grazed / ungrazed + housing	2 yr	n/a	
Bonte et al. (2000)	Belgium	coastal dunes	spiders	hist.	cattle / rabbit grazed	1 yr	n/a	
Boulton et al. (2005)	United States	serpentine grassland	ants	hist.	grazed / ungrazed	1 yr	17 yr	
Branson and Sword (2010)	United States	prairie	grasshoppers	exp.	rotational / ungrazed + burning	4 yr	2 yr	
Brown et al. (1992)	United Kingdom	restored calcareous grassland	leafhoppers	exp.	spring grazed / autumn grazed / both / ungrazed	1 yr	6 yr	
Cagnolo et al. (2002)	Argentina	montane grassland	beetles	exp.	intensive / extensive / short term ungrazed / long term ungrazed	1 yr	>7 yr	

Table A1. continued

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
Calcaterra et al. (2010)	Argentina	savanna/ floodplains	ants	exp.	grazed / ungrazed	2 yr	1 yr	y
Carvell (2002)	United Kingdom	calcareous grassland	bumblebees	hist.	sheep grazed / cattle grazed / abandoned + other micro environments	1 yr	n/a	y
Dahms et al. (2010)	Sweden	semi-natural grassland	ants	hist.	continuous grazing / abandoned / restored grazing	1 yr	n/a	
D'Anniello et al. (2011)	Italy	semi-natural grassland	butterflies	hist.	grazed / mown	2 yr	n/a	
Debinski et al. (2011)	United States	prairie	ants, butterflies, leafbeetles	exp.	grazed+burnt / patchburn +grazed / burn only	3 yr	1-3 yr	
Dennis et al. (1997)	United Kingdom	upland acid grassland	ground beetles, rove beetles	exp.	intensive sheep / extensive sheep / intensive sheep+cattle / extensive sheep+cattle / ungrazed	2 yr	2 yr	
Dennis et al. (1998)	United Kingdom	upland acid grassland	beetles, arachnids, moths, true bugs, leafhoppers	hist.	grain size of grazed mosaic	1 yr	4 yr	
Dennis et al. (2001)	United Kingdom	upland acid grassland	arachnids	exp.	intensive sheep / extensive sheep / intensive sheep+cattle / extensive sheep+cattle / ungrazed	2 yr	2 yr	y
Dennis et al. (2002)	United Kingdom	upland acid grassland	ground beetles, rove beetles	exp.	intensive sheep / extensive sheep / intensive sheep+cattle / extensive sheep+cattle / ungrazed	2 yr	2 yr	
Dennis et al. (2004)	United Kingdom	production grassland	beetles	exp.	intensive / extensive + cessation of N fertilisation	2 yr	0,2 yr	
Desender et al. (1999)	Galapagos	volcano gradient	beetles, spiders	hist.	damaged / undamaged	2 yr	10 yr	
Dolek and Geyer (1997)	Germany	hay meadows and fens	butterflies	hist.	grazed / mown	1 yr	n/a	
Dumont et al. (2009)	France	upland acid grassland	butterflies, grasshoppers	exp.	high / intermediate / low grazing	5 yr	1 yr	y
Eyre et al. (2003)	United Kingdom	heathland	ground beetles, rove beetles, spiders, true bugs	hist.	grazed / ungrazed + herbicide and burning	5 yr	n/a	

Table A1. continued

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
Fabriciusova et al. (2011)	Slowakia	montane grassland	grasshoppers	hist.	permanent grazing / temporal grazing	1 yr	n/a	
Fadda et al. (2008)	France	steppe	beetles	exp.	grazed / ungrazed	2 yr	23yr	y
Farruggia et al. (2012)	France	upland grassland	butterflies	exp.	rotational / continuous grazing	4 yr	1 yr	
Fisher Barham and Stewart (2005)	United Kingdom	calcareous grassland	leafhoppers	exp.	sheep / rabbit / ungrazed	1 yr	7 yr	Y*
Foote and Rice Horning (2005)	Canada	prairie	dragonflies	hist.	rotational / continuous / ungrazed	2 yr	n/a	
Ford et al. (2013)	United Kingdom	coastal salt marsh	beetles, spiders, true bugs, leafhoppers	hist.	grazed / ungrazed	1 yr	n/a	
Franzen and Nilsson (2008)	Sweden	semi-natural grasslands	butterflies, bees	hist.	grazed / ungrazed	2 yr	n/a	
Frennette-Dussault et al. (2013)	Morocco	steppe	ants	exp.	grazed / ungrazed + aridity gradient	1 yr	n/a	
Gardner et al. (1997)	United Kingdom	heathland	ground beetles	hist.	gradient of grazing intensity	1 yr	n/a	
Gebeyehu and Samways (2002)	South Africa	savannah	grasshoppers	hist.	wild herbivores / livestock	1 yr	n/a	
Gebeyehu and Samways (2003)	South Africa	savannah	grasshoppers	exp.	seasonal / rotational / resting / continuous	2 yr	>10 yr	
Gibson et al. (1992)	United Kingdom	restored calcareous grassland	herbivorous beetles, true bugs	exp.	spring grazed / autumn grazed / both / ungrazed	5 yr	1,2,4,5	y [†]
Gibson et al. (1992)	United Kingdom	restored calcareous grassland	spiders	exp.	spring grazed / autumn grazed / both / ungrazed	5 yr	1,2,4,5	
Gómez and González-Megías (2007)	Spain	alpine meadow	all herbivores on one plant	exp.	grazed / ungrazed	6 yr	1 yr	
González-megías et al. (2004)	Spain	alpine meadow	beetles, ants	exp.	grazed / ungrazed	2 yr	3 yr	
Grandchamp et al. (2005)	Switzerland	alpine meadow	ground beetles	hist.	grazed / mown + fertilisation	2 yr	n/a	
Gudleifsson and Bjarnadottir (2004)	Iceland	semi-natural grassland	beetles	exp.	grazed / mown + 3 soiltypes	1 yr	n/a	
Hartley et al. (2003)	United Kingdom	heathland	leafhoppers	exp.	grazed / ungrazed + fertiliser	2 yr	0-2 yr	
Hatfield and LeBuhn (2007)	United States	semi-natural grassland	bumblebees	hist.	sheepgrazed / cattle grazed / ungrazed	2 yr	n/a	
Hoffmann and James (2011)	Australia	chenopod scrubland	ants	hist.	gradient from water source	1 yr	n/a	
Hofmann and Mason (2006)	United Kingdom	coastal grazing marsh	rove beetles	hist.	gradient of grazing intensity + mowing + ungrazed	1 yr	n/a	

Table A1. continued

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
Holmes et al. (1979)	Canada	fescue grassland	grasshoppers	exp.	gradient of grazing intensity	7 yr	20 yr	
Holmes et al. (1993)	United Kingdom	peatland	ground beetles	hist.	intensive / extensive / ungrazed	3 yr	n/a	
Holmquist et al. (2013)	United States	subalpine grasslands	ants	exp.	grazed / ungrazed + early and mid-season	2 yr	1 yr	
Horváth et al. (2009)	Hungary	sandy grasslands	spiders	hist.	gradient of grazing intensity	3 yr	n/a	
Hutton and Giller (2003)	Ireland	semi-natural grassland	dung beetles	hist.	intensive / rough grazing / organic farming	1 yr	>3 yr	
Jankielsohn et al. (2001)	South Africa	grassveld, bushveld	dung beetles	hist.	wild herbivores / livestock	1 yr	n/a	
Jansen et al. (2013)	South Africa	montane grassland	spiders	hist.	wild herbivores / livestock	1 yr	± 30 yr	
Jáuregui et al. (2008)	Spain	heathland	grasshoppers	exp.	intensive / extensive x 2 goat breeds	3 yr	1 yr	y
Jay-Robert et al. (2008)	France	semi-natural grassland, scrubland, forest	dung beetles	hist.	wild herbivores / extensive livestock	2 yr	n/a	
Jepson-Innes and Bock (1989)	United States	arid grassland	grasshoppers	exp.	grazed / ungrazed	1 yr	15 yr	
Joern (2004)	United States	prairie	grasshoppers	exp.	grazed / ungrazed + burning	1 yr	>10 yr	
Joern (2005)	United States	prairie	grasshoppers	exp.	gradient of grazing intensity + burning	1 yr	10 yr	
Jonas and Joern (2007)	United States	prairie	grasshoppers	exp.	grazed / ungrazed + burning	23 yr	1 yr	
Kaltsas et al. (2013)	Greece	scrubland	ground beetles	hist.	gradient of grazing intensity	1 yr	n/a	
Kati et al. (2012)	Greece	seasonally flooded grasslands	butterflies, grasshoppers	hist.	grazed, mown, construction site	1 yr	n/a	
Kearns and Oliveras (2009)	United States	urban grassland	bees	hist.	grazed / ungrazed	1 yr	n/a	
Kleintjes Neff et al. (2007)	Canada	grassland/ forest	butterflies	exp.	grazed / ungrazed	4 yr	1-4 yr	
Körösi et al. (2013)	Hungary	steppe	true bugs, leafhoppers	hist.	intensive / extensive	1 yr	n/a	
Kruess and Tschardtke (2002a)	Germany	semi-natural grassland	beetles, true bugs, leafhoppers, parasitic wasps	hist.	intensive / extensive / short term ungrazed / long term ungrazed	1 yr	n/a	y†
Kruess and Tschardtke (2002b)	Germany	semi-natural grassland	butterflies, grasshoppers, wasps	hist.	intensive / extensive / ungrazed	1 yr	n/a	y†
Lenoir and Lennartson (2010)	Sweden	semi-natural grassland	ground beetles, ants, spiders	exp.	all season / late season grazed	1 yr	2 yr	

Table A1. continued

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
Littlewood (2008)	United Kingdom	upland acid grassland	moths	exp.	intensive sheep / extensive sheep / extensive sheep+cattle / ungrazed	1 yr	5 yr	
Littlewood et al. (2013)	United Kingdom	upland acid grassland	leafhoppers	exp.	intensive sheep / extensive sheep / extensive sheep+cattle / ungrazed	1 yr	>5 yr	
Lumaret et al. (1992)	France	Mediterranean grassland	dung beetles	exp.	sheep / cattle grazed	4 yr	3 yr	
Macagno and Palestini (2009)	Italy	alpine meadow	dung beetles	hist.	grazed / ungrazed	1 yr	n/a	
Meyer et al. (1995)	Germany	coastal salt marsh	beetles, spiders, leafhoppers, true bugs	exp.	intensive / moderate / extensive / low / ungrazed	3 yr	1 yr	
Miller and Onsager (1991)	United States	prairie	grasshoppers	hist.	intensive / extensive / ungrazed	1 yr	n/a	
Moran et al. (2012)	Ireland	turloughs	ground beetles	hist.	grazed / ungrazed + two vegetation types	3 yr	0 yr	
Moranz et al. (2012)	United States	prairie	butterflies	exp.	grazed+burnt / patchburn +grazed / burn only	2 yr	1 yr	
Morris (1967)	United Kingdom	calcareous grassland	all herbivores on one plant	exp.	grazed / ungrazed	2 yr	2 months	
Morris (1969)	United Kingdom	calcareous grassland	true bugs	exp.	grazed / ungrazed	4 yr	4 months	
Morris (1971)	United Kingdom	calcareous grassland	leafhoppers	exp.	grazed / ungrazed	2 yr	2 yr	
Morris (1973)	United Kingdom	calcareous grassland	true bugs, leafhoppers	exp.	spring grazed / summer grazed / autumn grazed / winter grazed / ungrazed	4 yr	2 yr	
Morris et al. (2005)	United Kingdom	calcareous grassland	leafhoppers	exp.	rotational grazing	9 yr	2 yr	
Mysterud et al. (2010)	Norway	alpine meadow	beetles, spiders	exp.	intensive / extensive / ungrazed	1 yr	2 yr	y*
Nash et al. (2004)	United States	desert	ants	hist.	gradient from water source	1 yr	n/a	
Negro et al. (2011)	Italy	alpine meadow	dung beetles	hist.	overgrazed / ungrazed	1 yr	n/a	
Ni Bhriain et al. (2002)	Ireland	turloughs	ground beetles	hist.	grazed / ungrazed	1 yr	n/a	y
Nickel and Hildebrandt (2003)	Germany	floodplain meadow	leafhoppers	hist.	intensive / extensive / ungrazed	2 yr	n/a	
Noel and Finch (2010)	Norway	alpine meadow	spiders	hist.	grazed / ungrazed	1 yr	n/a	
Öckinger et al. (2006)	Sweden	semi-natural grassland	butterflies	hist.	restored / abandoned	1 yr	n/a	y

Table A1. continued

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
O'Neill et al. (2003)	United States	prairie	grasshoppers	exp.	intensive / extensive (mosaic vegetation) / ungrazed	5 yr	1 yr	
O'Neill et al. (2010)	United States	prairie	grasshoppers	exp.	intensive / extensive (mosaic vegetation) / ungrazed	6 yr	1 yr	
Onsager (2000)	United States	prairie	grasshoppers	exp.	rotational / continuous	5 yr	1-6 yr	
Paschetta et al. (2012)	Italy	alpine meadow	spiders	hist.	intensive / extensive / ungrazed	1 yr	n/a	
Pétillon et al. (2007)	France	coastal salt marsh	ground beetles, spiders	hist.	grazed / ungrazed	1 yr	n/a	
Pihlgren et al. (2010)	Sweden	semi-natural grassland	ants	hist.	grazed / ungrazed + exposition	1 yr	n/a	y
Pöyry et al. (2004)	Finland	semi-natural grassland	butterflies	hist.	historic grazing / abandoned / restored grazing	2 yr	>5 yr	y§
Pöyry et al. (2005)	Finland	semi-natural grassland	butterflies	hist.	historic grazing / abandoned / restored grazing	2 yr	>5 yr	
Pöyry et al. (2006)	Finland	semi-natural grassland	butterflies	hist.	historic grazing / abandoned / restored grazing	1 yr	n/a	
Prendini et al. (1996)	South Africa	savannah	grasshoppers	hist.	wild herbivores / livestock	1 yr	> 15 yr	y
Purvis and Curry (1981)	Ireland	semi-natural grassland	beetles, spiders, true bugs, leafhoppers, thrips	exp.	continuous grazing / intermittent grazing + mowing	1 yr	2 yr	
Quinn and Walgenbach (1990)	United States	prairie	grasshoppers	hist.	wild herbivores / livestock / ungrazed	1 yr	n/a	
Rickert et al. (2012)	Germany	coastal salt marsh	moths	exp.	intensive / moderate / extensive / ungrazed	4 yr	17 yr	y
Rosa-Garcia et al. (2009a)	Spain	heath scrubland	ground beetles, arachnids	exp.	intensive (2 cattle breeds) / extensive (1 breed)	3 yr	2 yr	
Rosa-Garcia et al. (2009b)	Spain	heath scrubland	ground beetles, arachnids	exp.	intensive (2 cattle breeds) / extensive (1 breed) / ungrazed	5 yr	2 yr	
Saarinén and Jantunen (2005)	Russia/ Finland	boreal grassland	butterflies	hist.	grazed / mown	3 yr	n/a	
Saarinén (2002)	Finland	semi-natural grassland	butterflies	hist.	traditionally grazed / intensive grazing / mowing	3 yr	n/a	

Table A1. continued

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
Samways and Kreutzinger (2001)	South Africa	savannah	grasshoppers	hist.	wild herbivores / livestock	1 yr	n/a	
Schmidt et al. (2012)	Canada	semi-arid grassland	ants	exp.	grazed / ungrazed	2 yr	20 yr	
Schohier and Dumont (2013)	France	upland grassland	butterflies and bumblebees	exp.	continuous / rotational (within season) grazing	2 yr	0 yr	
Sjödín (2007)	Sweden	semi-natural grassland	but-terflies, bees, hoverflies	exp.	all season / late season grazed	1 yr	2/5 yr	
Sjödín et al. (2008)	Sweden	semi-natural grassland	but-terflies, bees, hoverflies	hist.	intensive / extensive / ungrazed	1 yr	n/a	y
Smith (1940)	United States	prairie	beetles, bees, grasshoppers, true bugs, flies, leafhoppers, other Hymenoptera, other groups	hist.	gradient from lightly grazed to heavily overgrazed	1 yr	n/a	y
Söderström et al. (2001)	Sweden	semi-natural grassland	butterflies, ground beetles, bumblebees, dung beetles	hist.	gradient of grazing intensity	2 yr	n/a	
Spalinger et al. (2012)	Switzerland	alpine meadow	grasshoppers	hist.	grazer induced variation in vegetation height	1 yr	n/a	
Sterling et al. (1992)	United Kingdom	restored calcareous grassland	leaf miners (Diptera & Lepidoptera)	exp.	spring grazed / autumn grazed / both / ungrazed	5 yr	1 yr	
Stoner and Joern (2004)	United States	prairie	butterflies, grasshoppers, weevils, lady birds,	hist.	grazed / mown	1 yr	n/a	
Swengel (1998)	United States	prairie	butterflies	hist.	grazed / mown + burning	8 yr	n/a	
Szinétár and Samu (2012)	Hungary	dry grassland	spiders	exp.	intensive / extensive / ungrazed	2 yr	1 - 3 years after	
Underwood and Christian (2009)	United States	Mediterranean grassland	ants	exp.	grazed / ungrazed	1 yr	1 yr	
Van Noordwijk et al. (2012), chapter 3	Netherlands	calcareous grassland	ants	hist.	historic / restored grazing	1 yr	n/a	
Verdu et al. (2007)	Mexico	xeric grassland	dung beetles	hist.	grazed / ungrazed	1 yr	n/a	
Vogel et al. (2007)	United States	prairie	butterflies	exp.	grazed / ungrazed + burning	2 yr	> 4 yr	
Vulliamy et al. (2006)	Israel	steppe	bees	hist.	gradient of grazing intensity	1 yr	n/a	
WallisDeVries and Raemakers (2001)	Netherlands	coastal dunes	butterflies	hist.	grazed / ungrazed	4 yr	n/a	

Table A1. continued

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment	Used for quantitative review
WallisDeVries et al. (2007)	United Kingdom, France, Germany, Italy	various	butterflies, grasshoppers	exp.	moderate / lenient	3 yr	1 yr	y*
Warui et al. (2005)	Kenia	savannah	spiders	exp.	grazed / ungrazed	1 yr	6 yr	
Weiss et al. (2013)	Germany	calcareous grassland	grasshoppers	hist.	grazed / mown + exposition	1 yr	n/a	
Wettstein and Schmid (1999)	Switzerland	montane wetlands	butterflies, grasshoppers	hist.	grazed / mown + altitude	1 yr	n/a	
Whitford et al. (1999)	United States	desert grassland	ants	hist.	ungrazed / continuously / seasonally grazed	1 yr	up to 46 years	
Woodcock et al. (2005)	United Kingdom	calcareous grassland	beetles	hist.	long- / short-term rotational grazing with sheep / cattle / ungrazed	1 yr	n/a	
Woodcock et al. (2006)	United Kingdom	floodplain meadow	beetles	exp.	cattle / sheep / ungrazed	1 yr	18 yr	y
Xie et al. (2008)	China	alpine meadow	bumblebees	hist.	grazed / ungrazed	2 yr	n/a	
Yoshihara et al. (2008)	Mongolia	steppe	but-terflies, bees, hoverflies	hist.	intensive / extensive / ungrazed	1 yr	n/a	
Zhu et al. (2012)	China	steppe	butterflies, grasshoppers, beetles, moths, true bugs, bees, leafhoppers, other groups	exp.	intensive / extensive / ungrazed + plant diversity gradient	1 yr	2 yr	
Zulka et al. (1997)	Austria	inland salt marsh	spiders	hist.	grazed / ungrazed	1 yr	1 yr	
Zürbrugg and Frank (2006)	Switzerland	ex-arable land	true bugs	exp.	sown flowers / cattle grazed / mown	1 yr	3 yr	y*

* Plant diversity response data obtained from the authors.

† Plant diversity response data obtained from Mortimer et al. (1998).

‡ Diversity response of different arthropod groups was pooled from these publications, plant diversity response was obtained from (Kruess and Tschamntke 2002a)

§ Plant diversity response data obtained from Pykälä (2003).

Appendix 2. Studies on herbivore effects in woodlands

Table A2. Studies on effects of large herbivores on arthropod diversity in wood- and shrub lands. Criteria for inclusion were the same as for Appendix 1. Abbreviations as in Table A1.

Reference	Country	Ecosystem	Group	Type of experiment	Treatments	Duration of study	Time after start of experiment
Abensperg-Traun et al. 1996	Australia	Eucalyptus forest	termites, ants	hist.	grazed (in classes) / ungrazed	1 yr	na
Bestelmeyer and Wiens (1996)	Argentina	xerophyllous subtropical forest	ants	hist.	degraded, moderately / half restored / fully restored	1 yr	na
Botes et al. (2006)	South Africa	sand forest	dung beetles	exp.	disturbed / not disturbed	2 yr	na
Danell and Huss-Danell (1985)	Sweden	Salix meadow	all insects on one plant species	hist.	slightly / moderately browsed	1 yr	na
Den Herder et al. (2004)	Finland	tundra	all insects on one plant species	exp.	grazed / ungrazed	2 yr	4,5
Melis et al. (2006)	Norway	boreal mixed forest	ground beetles	hist.	intensive / extensive / ungrazed	1 yr	na
Melis et al. (2007)	Norway	boreal mixed forest	ground beetles	hist.	different browsing intensities	1 yr	na
Roininen et al. (1997)	Alaska	boreal mixed forest	sawflies and other gallers	exp.	browsed / unbrowsed	1 yr	3 yr
Suominen et al. (2003)	Finland	boreal mixed forest	weevils, ground beetles	exp.	grazed / ungrazed	1 yr	>5 yr
Suominen et al. (1999)	Sweden	boreal mixed forest	spiders, beetles, harvestmen	exp.	browsed / unbrowsed	1 month	15 yr
Vazquez and Simberloff (2002)	Argentina	Nothofagus forest	flower visitors	hist.	grazed / ungrazed	1 yr	na
Vazquez and Simberloff (2003)	Argentina	Nothofagus forest	flower visitors	hist.	grazed / ungrazed	1 yr	na

Appendix 3. Definitions of taxonomic groups

Ground beetles*: Coleoptera: Carabidae;

Grasshoppers: Orthoptera;

Butterflies: day-active Lepidoptera (Papilionoidea & Hesperoidea), plus day-active moths;

Rove beetles*: Coleoptera: Staphylinidae;

Arachnids: Araneae, Opiliones, Pseudoscorpiones (Acari excluded);

Leafhoppers: Hemiptera: Auchenorrhyncha (Fulgoromorpha & Cicadomorpha);

True bugs: Hemiptera: Heteroptera;

Dung beetles*: Coleoptera: Scarabaeoidea;

Bees: Hymenoptera: Apidae & Bombidae;

Moths: all nocturnal Lepidoptera;

Other beetles*: all other Coleoptera. Mostly herbivorous families (Coleoptera: Chrysomelidae & Curculionidae);

Hoverflies: Diptera: Syrphidae;

Ants: Hymenoptera: Formicidae;

Other Hymenoptera: all non apid or formicid Hymenoptera;

Other flies: non syrphid Diptera;

Dragonflies: Odonata;

Termites: Isoptera;

Thrips: Thysanoptera;

Other groups: Neuroptera, Phasmatodea, Mantodea

* Because many studies report results on only one family of beetles (Carabidae or Staphylinidae), we scored all studies reporting on all beetles as three taxa: Carabidae, Staphylinidae and other beetles. Dung beetles were, however, scored only when appropriate sampling methods for this group had been used (baited pitfall traps or dung collection).

Young *Glanville fritillaria* (*Melitaea cinxia*) caterpillars (Photo: Toos van Noordwijk)



Chapter 5

Impact of grazing management on hibernating caterpillars of the butterfly *Melitaea cinxia* in calcareous grasslands

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Abstract

Semi-natural grasslands are increasingly grazed by large herbivores for nature conservation purposes. For many insects such grazing is essential for the conservation of their habitat, but at the same time, populations decrease at high grazing intensity. We hypothesised that grazing management may cause increased butterfly mortality, especially for life-stages with low mobility, such as hibernating caterpillars. To test this, we measured the effect of sheep grazing on overwinter larval survival. We used the Glanville fritillary (*Melitaea cinxia*), which has gregarious caterpillars hibernating in silk nests, as a model species. Caterpillar nests were monitored throughout the hibernating period in calcareous grassland reserves with low and high intensity sheep grazing and in an ungrazed control treatment. After grazing, 64% of the nests at the high intensity grazing treatment were damaged or missing, compared to 8% and 12% at the ungrazed and low intensity grazing treatment, respectively. Nest volume and caterpillar survival were 50% lower at the high intensity grazing treatment compared to both ungrazed and low intensity grazing treatments. Nest damage and increased mortality were mainly caused by incidental ingestion of the caterpillars by the sheep. It is likely that grazing similarly affects other invertebrates, depending on their location within the vegetation and their ability to actively avoid herbivores. This implies that the impact of grazing strongly depends on the timing of this management in relation to the phenology of the species. A greater focus on immature and inactive life-stages in conservation policy in general and particularly in action plans for endangered species is required to effectively preserve invertebrate diversity.

Keywords

Life-history trait, invertebrate biodiversity, butterfly conservation, Lepidoptera, herbivore predation, incidental omnivory.

Introduction

Nutrient-poor, semi-natural grasslands harbour a large part of the biodiversity in temperate climates, especially for plants and insects (Stevens et al. 2004; WallisDeVries et al. 2002). Biodiversity in these grasslands depends strongly on management, such as grazing or cutting (Baldock et al. 1996; Morris 2000; Ostermann 1998; Willems 2001). Management is essential to prevent encroachment of tall grasses, shrubs and trees and it facilitates the development of a heterogeneous vegetation structure that provides a suitable habitat for numerous plant and animal species (Morris 2000; Morris et al. 1990; Willems 2001). Historically, management in most semi-natural grasslands in Western Europe consisted of low-intensity farming practices (Ostermann 1998; Poschlod and WallisDeVries 2002). Over the past century, agricultural intensification and the introduction of artificial fertilizers have led to abandonment of these farming practices and conversion of semi-natural grasslands to arable land and high intensity agricultural grassland (Baldock et al. 1996). This resulted in a strong decline in species richness (Stevens et al. 2004; Van Swaay et al. 2010; WallisDeVries et al. 2002). In addition, absence of management in remaining sites has led to severe grass, shrub and tree encroachment, causing plant and insect species richness to decline even further (Dover et al. 2011; WallisDeVries et al. 2002; Willems 2001). In many sites the problems caused by fragmentation and abandonment were further amplified by eutrophication from both adjacent agricultural areas (run-off) and airborne nitrogen pollution (Bobbink and Willems 1993; Willems 2001). These land use changes resulting from abandonment of traditional agricultural practices across Europe are believed to be one of the largest threats to European butterflies (Van Swaay et al. 2010).

To counter the negative effects of abandonment on grassland biodiversity, remaining semi-natural grasslands are now increasingly managed for nature conservation purposes (Ostermann 1998) or included in agri-environment schemes (WallisDeVries et al. 2007; Konvicka et al. 2008). Conservation management of semi-natural grasslands usually consists of mowing or grazing with large herbivores. These new management practices often lead to conflicting interests, because various taxonomic groups differ in their response to particular management measures (Kruess and Tscharntke 2002a; Oertli et al. 2005; Vessby et al. 2002). The reason for this conflict is that current management, although necessary for the conservation of semi-natural habitats, can be detrimental to part of the characteristic species of semi-natural grasslands (Carvell 2002; Humbert et al. 2010; Morris 2000; Morris et al. 1990). Insects in general (Bourn and Thomas 2002; Kruess and Tscharntke 2002a; Mortimer et al. 1998; Samways 1994) and especially butterflies (Franzén and Ranius 2004; Schtickzelle et al. 2007a; Konvicka et al. 2008) have proven to be very sensitive to some management measures. This demonstrates the need for appropriate action plans in which specific attention is paid to the needs of grassland butterflies.

There is growing evidence from nature conservation research that the impact of management practices on species strongly depends on their life-cycle and associated traits (Van Kleef et al. 2006; Verberk et al. 2008b; chapter 3). To what extent a species can escape temporarily unfavourable conditions is determined by its mobility (Dennis et al. 1998; Siepel 1995; Van Kleef et al. 2006), while its microhabitat (e.g. height within the meadow vegetation strata) determines to what extent species are affected by grazing or mowing

management (Humbert et al. 2009). In species with distinct periods of larval and adult activity the impact of a management measure also strongly depends on management timing in relation to the phenology of the species (Konvicka et al. 2008; Humbert et al. 2009; Morris 1973; Morris et al. 1990). To estimate the impact of management practices in relation to species traits, it is essential to incorporate the requirements of all life-stages and to evaluate which life-stages will actually be affected (i.e. will be present during the management period). It is widely acknowledged that the requirements of eggs and larval stages are often more demanding than those of the adult stages (Bourn and Thomas 2002; Fartmann and Hermann 2006). Eggs and larval stages of most insects are also considerably less mobile than adult stages (Bourn and Thomas 2002), making them more vulnerable, as they cannot escape temporarily unfavourable conditions (Dennis et al. 1998).

In practice, few conservation management plans, including European agri-environment schemes, explicitly incorporate the importance of species' life-history traits and the particular vulnerability of immature stages (see Aviron et al. 2010; Pywell et al. 2011). Scientific studies investigating negative effects of conservation management on butterflies have predominantly addressed larval habitat requirements indirectly, by focussing on changes in adult abundance and relating these to changes in vegetation structure or food availability (Kruess and Tschardt 2002b; Poyry et al. 2006; Schtickzelle et al. 2007a; WallisDeVries et al. 2007). This focus may result in an incomplete assessment of larval habitat quality and bias management towards the needs of adult life stages. Recommendations resulting from these studies often emphasize to decrease management intensity during the adult flight season and increase management efforts in autumn and winter when species are hibernating as immature stages (Ellis 2003; Morris 1973; Oates 1995; Schtickzelle et al. 2007a). From a life-history trait perspective these immature and inactive life-stages may, however, be even more vulnerable to mowing or grazing management than their adult counterparts. Actual data on the impact of management on the larval stages are therefore urgently required to improve butterfly conservation (Fartmann and Hermann 2006; Thomas et al., 2011).

The aim of our study was to quantify the direct effects of autumn grazing on hibernating caterpillars and to shed light on the underlying mechanisms. The ensuing information could prove essential to arrive at more effective management schemes for conservation. We hypothesised that grazing management may cause increased mortality in hibernating caterpillars. Hibernating caterpillars were expected to be unable to escape grazing animals and may therefore be trampled or ingested. We expected that caterpillar mortality would increase with increasing grazing intensity as this would lead to increased encounter rates. These hypotheses were tested with a field experiment, using the Glanville fritillary (*Melitaea cinxia*) in calcareous grasslands grazed by sheep as a model system. The Glanville fritillary was chosen as a model species because it has gregarious caterpillars hibernating in silk nests that are more easily retraced than individual caterpillars (Hanski 1999; WallisDeVries 2006).

Methods

Site description

The experiment was conducted on two calcareous grasslands differing in sheep grazing intensity, near the city of Maastricht; Thier de Lanaye (Belgium) and Bemelerberg (the Netherlands). Thier de Lanaye (50° 46' 41" N, 5° 40' 45" E, altitude 80 m) is situated on the west-bank of the Meuse valley and consists of grassland (4 ha) surrounded by deciduous woods. The calcareous grassland is divided into five sections by permanent fencing, which are grazed separately in one or more rounds between April and October each year. Our experiment was conducted in one of these sections (size 0.5 ha, slope 23 °, aspect south-east), which is only grazed in autumn at low stocking densities. Bemelerberg (50° 51' 03" N, 5° 46' 09" E, altitude 90 m) is located about 10 km northeast of Thier de Lanaye on the north-bank of a dry valley. This site consists of a number of calcareous grasslands interspersed with deciduous woodland and agricultural fields. The grassland section used in this experiment (size 4 ha, slope 20 °, aspect south-east) is grazed at high stocking densities in autumn with additional spring grazing (high stocking densities) and winter grazing (low stocking densities) in some parts. Both study sites are grazed with a local, traditional sheep breed (Mergelland).

Study species

Field studies on larval survival are hampered by the difficulty to monitor individual caterpillars in the field. This difficulty was overcome here by using a species with gregarious caterpillars, the Glanville fritillary (*Melitaea cinxia*), as a model species. *Melitaea cinxia* was primarily chosen because of its gregariously hibernating caterpillars, which make it easier to study the caterpillars throughout the season in the field. We expected that the mechanistic understanding provided by this type of research would enable us to evaluate to what extent the results can be extrapolated to other non-gregarious species. In any case this research would provide valuable information for other gregariously hibernating butterfly species, including the highly threatened Marsh fritillary (*Euphydryas aurinia*), which is a European Habitats Directive species (Smee et al. 2011).

Melitaea cinxia is a characteristic butterfly of calcareous, to slightly acidic dry grasslands. They are especially found in sites with substantial variation in vegetation structure and a high abundance of flowering plants (Bink 1992; Kuussaari 1998; WallisDeVries 2006). The species has a large Eurasian distribution (Bink 1992), its northern limit coincides with a July isotherm of 16.5–17.0 °C. The flight period of *M. cinxia* peaks between mid-May and mid-June (Bink 1992). Oviposition typically occurs in clusters of 100–200 eggs on the underside of the leaves of its host plant, predominantly ribwort plantain (*Plantago lanceolata*) in northwestern Europe. The caterpillars hibernate gregariously in a densely woven silk nest in tufts of grass (WallisDeVries 2006), typically 5–10 cm above the ground (personal observation). The larvae remain gregarious in spring until the final instar. The population of *M. cinxia* at Thier de Lanaye was reintroduced in 1997 (Goffart et al. 2001). The population at Bemelerberg was established in 2007 from

an introduction of fourteen larval nests from Thier de Lanaye. In the first year after introduction part of the grassland containing most caterpillar nests was fenced off during grazing in autumn.

Nest selection and experimental design

Melitaea cinxia nests were searched in both study sites on three occasions between 15th July and 25th August 2009 (Figure A1 & A2). Each nest was marked by placing a 50 cm long PVC pole next to it. Nest locations were mapped (accuracy 10cm) using a grid of fixed poles with known GPS coordinates and ArcGIS 9.1 software. In total 120 nests were found at the high intensity grazing site (Bemelerberg) and 41 at the low intensity grazing site (Thier de Lanaye). The volume of each nest was calculated from length $\times$ height $\times$ width measurements that were taken using a vernier calliper. At the low intensity grazing site we selected the 25 largest nests for subsequent monitoring. At the high intensity grazing site the area containing the highest nest density was split in two and one half was fenced off using flexible electric fencing to form an ungrazed control treatment. These grazed and ungrazed plots at the high intensity grazing site were located next to each other and were very similar in slope, aspect and vegetation composition. Pairs of equally sized nests were selected for further monitoring in these two treatments, working from the largest nests down until we had selected 25 nests per treatment. Around each selected nest in both study sites we conducted an extensive search to detect and remove any other nests in the immediate vicinity. Nests that were less than 50 cm away from the selected nests were excluded and later physically removed from the experimental plots to enable accurate caterpillar counts per nest in spring. The final set-up consisted of three grazing treatments; low intensity grazing (Thier de Lanaye, 25 caterpillar nests), high intensity grazing (Bemelerberg, 25 caterpillar nests) and no grazing (exclosure Bemelerberg, 24 caterpillar nests). The treatments were not replicated in different sites as we did not have access to multiple sites with similar management and a sufficiently large population of the study species. Therefore, this experiment does not allow us to make general statements on the effects of the studied grazing intensities on caterpillar survival. Nonetheless, as caterpillar nests were at least 1 meter apart and grazing effects generally occur on a much smaller spatial scale (Parsons and Dumont 2003; Prache et al. 1998), the individual nests can be viewed as full replicates of the impact of grazing under the given circumstances. As the circumstances at the ungrazed and high intensity grazing treatment were equal except for the grazing treatment (the exclosure was especially erected for this experiment and the two treatments were located adjacent to each other), any differences found can be attributed to the grazing regime. Therefore, this study gives valuable insight in the effects grazing can have on hibernating caterpillars. The second site, with a different grazing regime, gives some insight in the generality of the effects of grazing.

Grazing was conducted in the second half of September in both grazed treatments (Table 1). At the high intensity grazing treatment, this was followed by a second grazing round at lower stocking densities. Prior to grazing all poles were removed to avoid attraction of the sheep to the nests. Instead, nests were individually marked with plastic arrows that were secured to the ground with nails and were placed at a distance of 30-70 cm from the nest. The arrows pointed towards the nest and had the nest ID and distance marked on them to facilitate nest searching. A number of nests of different sizes that

Table 1. Observed grazing intensity during the experiment in autumn 2009.

Treatment	Sheep (#)	Compartment size (ha)	Grazing period date (days)	Grazing intensity (sheep-days · ha ⁻¹)
No grazing	5*	0.15	Sept 26 (1)	<35
Low intensity grazing	26	0.52	Sept 17 to Sept 23 (6)	300
High intensity grazing				1353
round 1	114	1.23	Sept 17 to Sept 27 (10)	927
round 2	15	1.76	Sept 29 to Nov 18 (50)	426

* A group of 5 sheep managed to enter the enclosure forming the ungrazed control treatment overnight. They were detected and removed within one day and the fence was improved afterwards.

were not included in the experiment (20 nests at Bemelerberg and 5 nests at Thier de Lanaye), were used to test nest volume as a proxy for the number of caterpillars per nest. In August 2009 these nests were measured as described above and opened to count the caterpillars inside.

Nest monitoring

Nest volume, nest height and vegetation height at the nest location were measured for each nest before grazing started in September and after the first (October) and second (December) grazing round. Vegetation height at the nest location was also measured in March 2010. Nest volume was measured as described above. Nest height was defined as the height of the top of each nest above the ground and was measured with a ruler to the nearest mm. The vegetation height at each nest location was measured by carefully lowering a drop disk (10 cm diameter, weighing 8 g) directly above the nest. After every grazing round each single nest was visually inspected and photographed. Nests without any external signs of damage were classified as undamaged (Figure A3 & A4). Nests with small holes, signs of tear or signs of repair of the silken nest were classified as lightly damaged (Figure A5 & A6). Nests were classified as heavily damaged (Figure A7 & A8) if part of the nest was absent or so heavily damaged that caterpillars had fallen out of the nest. If nests could not be retrieved they were classified as missing. In spring (early March 2010), the number of caterpillars per nest was counted. These counts were conducted on the first sunny days of the season when the caterpillars were usually basking on top of or next to their nests. At this stage, nests were opened to count all living caterpillars inside.

Statistical analysis

To establish whether there were any differences between the treatments prior to grazing we tested for differences in vegetation height (ANOVA) and nest volume (t-tests). For a selection of nests ($n = 25$) we tested whether caterpillar density (number of caterpillars per nest volume) differed between the two study sites using a students t-test. Next, the relationship between the number of caterpillars and nest volume was explored with a Pearson correlation coefficient.

Changes in vegetation height over time were used as an objective measure of grazing intensity. Differences in vegetation height at each nest location (within subject factor) over time and between treatments (between subject factor) were explored using a repeated measures ANOVA (nest locations were fixed and individually marked). A Greenhouse-Geisser correction was used to correct for violations of sphericity (Greenhouse and Geisser 1959). To establish whether the vegetation height declined evenly, or alternatively declined especially at patches with short or long swards (grazing preference of the sheep), we correlated vegetation decline during the first grazing round to the original vegetation height (Pearson correlation coefficient).

Differences in nest damage between treatments were explored with non-parametric statistics. Additionally, we tested whether nest damage occurred especially in nests that were situated low (more vulnerable to trampling) or high (more vulnerable to incidental ingestion) in the vegetation (ANOVA). We also explored the vegetation height at each individual nest location after grazing, in relation to the height of the nest prior to grazing. This gave an indication of ingestion of whole or partial caterpillar nests by the sheep during grazing.

We explored differences in nest volume and spring caterpillar counts between treatments using parametric statistics (ANOVA and t-test with Tukey post-hoc tests). As the nest volume prior to grazing differed between the two study sites we used relative nest volume (percentage of the nest volume prior to grazing) and relative caterpillar count (number of caterpillars relative to the nest size prior to grazing).

To satisfy normal distribution conditions vegetation heights were natural logarithmic transformed and absolute and relative nest volumes were square root transformed. Where several pairwise tests were conducted together, critical p values were Bonferroni corrected to account for the number of tests performed. All statistical tests were performed using SPSS for windows 16.0.1.

Results

Vegetation height

Vegetation height at the caterpillar nest locations did not differ between treatments prior to grazing (ANOVA, $F_{2,71} = 2.1$, $p = 0.13$). Vegetation height declined during the experiment in all treatments (Figure 1, Repeated measures ANOVA, $F_{2,135} = 117.3$, $p < 0.001$). The rate of decline increased with increasing grazing intensity (interaction time * treatment, $F_{4,135} = 6.5$, $p < 0.001$). However, the percentage decline in vegetation height differed only between grazing treatments after the first grazing round (Kruskal-Wallis, $\chi^2 = 26.5$, $p < 0.001$), not after the second (Kruskal-Wallis, $\chi^2 = 1.9$, $p = 0.38$). The reduction in vegetation height during the first grazing round was strongly positively correlated to the vegetation height prior to grazing for each grazing treatment (Pearson Correlation, $r > 0.6$, $n > 23$, $p < 0.001$).

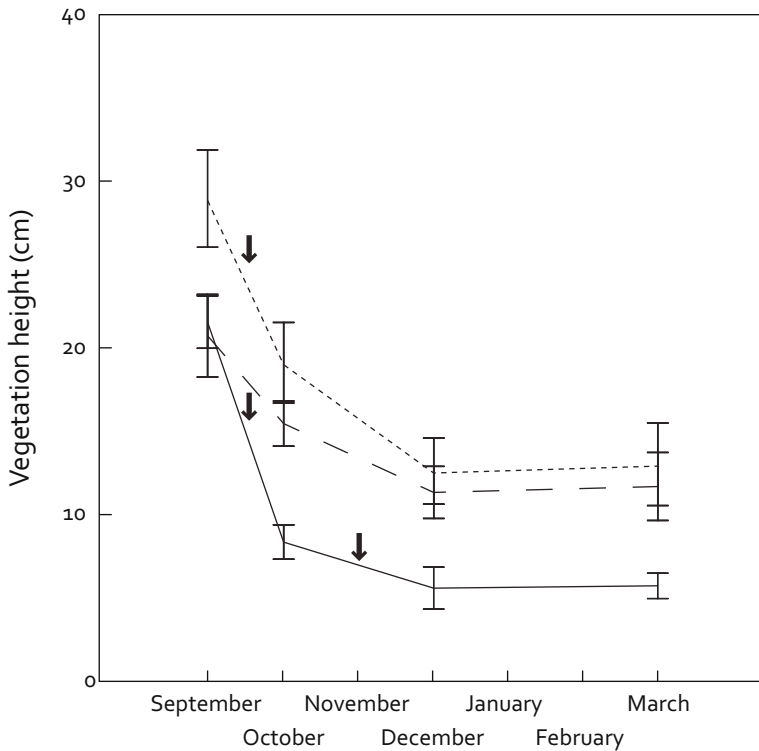


Figure 1. Mean vegetation height at the caterpillar nest locations (± 1.0 SE) prior to grazing (September), after the first grazing round (October), after the second grazing round (December) and after hibernation (March) for the high intensity grazing treatment (solid line), the low intensity grazing treatment (dotted line) and the ungrazed control treatment (dashed line). Grazing events are indicated with an arrow.

Nest survival and status

Overall nest survival was high, with all nests surviving until spring at the ungrazed treatment ($n = 24$), 96% nest survival at the low intensity grazing treatment ($n = 25$) and 88% nest survival at the high intensity grazing treatment ($n = 25$). In both grazed treatments one nest (4%) went missing during the first grazing round. Two more nests (8%) went missing in the high intensity grazing treatment during the second grazing round. After the first grazing round 60% (15 nests) of the nests at the high intensity grazing treatment appeared damaged, compared to 8% (2 nests) at both the ungrazed and low intensity grazing treatments (Figure 2). While nest status (i.e. number of nests per nest damage category) differed significantly between grazing treatments after the first grazing round (Kruskal-Wallis, $\chi^2 = 23.7$, $p < 0.001$; Table 2), no differences were found after the second grazing round (Kruskal-Wallis, $\chi^2 = 2.5$, $p = 0.28$).

Some of the damaged nests showed signs of trampling (nests lay near the ground and were flattened). In the high intensity grazing treatment three nests looked trampled after the first grazing round (20% of all damaged nests in this treatment), with two more nests

Table 2. Pairwise comparisons in nest status between treatments after the first grazing round (Bonferroni corrected critical $p = 0.01$).

Grazing treatment	Mann-Whitney U	Z	p
No grazing - Low intensity	288	-0.457	0.647
No grazing - High intensity	126	-4.062	<0.001
Low intensity - High intensity	150	-3.631	<0.001

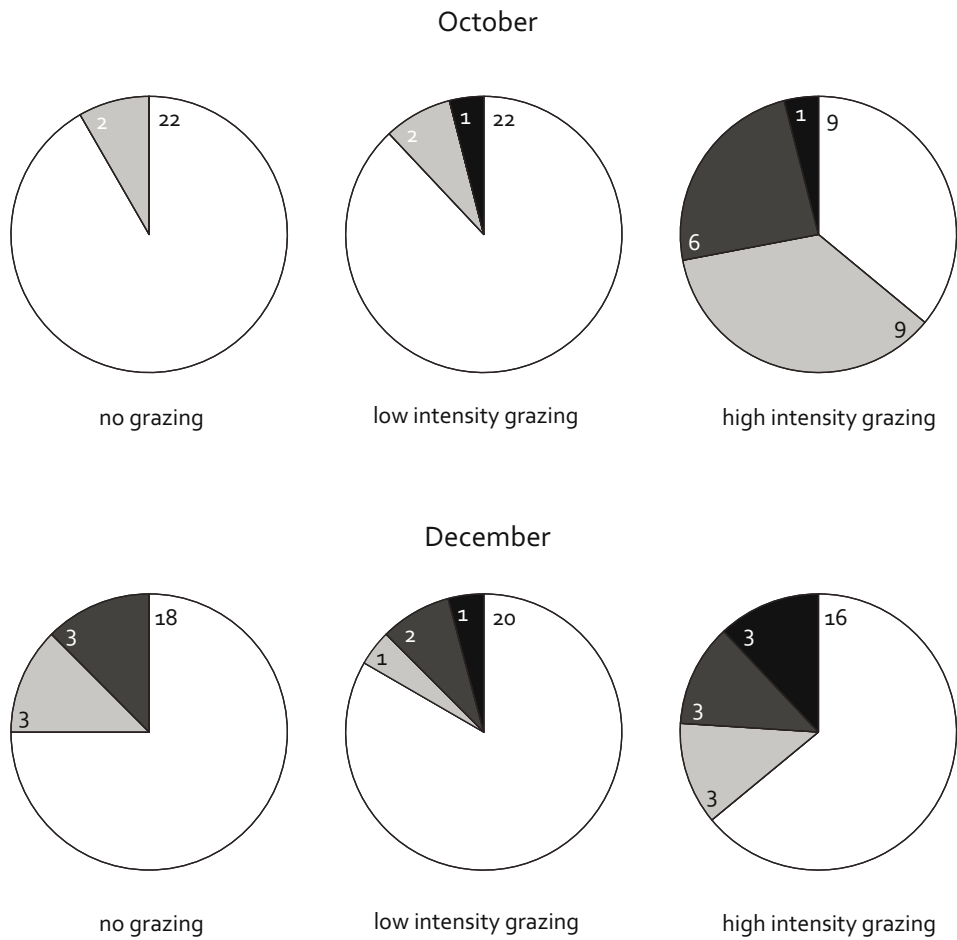


Figure 2. Distribution of undamaged (white), lightly damaged (light grey), heavily damaged (dark grey) and missing (black) nests per grazing treatment after the first (October) and second (December) grazing rounds.

showing trampling signs after the second grazing round. In the low intensity grazing treatment one nest showed signs of trampling after grazing. Overall, nest damage was unrelated to the height of the nest prior to grazing (ANOVA, $F_{3,70} = 0.84$, $p = 0.47$). However, there was a strong link between nest status and vegetation height after grazing. At damaged nests, vegetation height had decreased more strongly than at undamaged nests (t-test, $T_{72} = -6.56$, $p < 0.001$), indicating grazing activity. Exploration of the

vegetation height at each individual nest location after grazing, in relation to the height of the nest measured prior to grazing gave proof of incidental ingestion of caterpillar nests as a cause of the nest damage. At damaged nest sites, vegetation height had on average been reduced to 1.2 cm (± 1.8 SE, $n = 21$) below the nest height prior to grazing. In contrast, vegetation height at undamaged nest sites, was on average 7.9 cm (± 0.4 SE, $n = 53$) above the height of the nest prior to grazing (Figure 3).

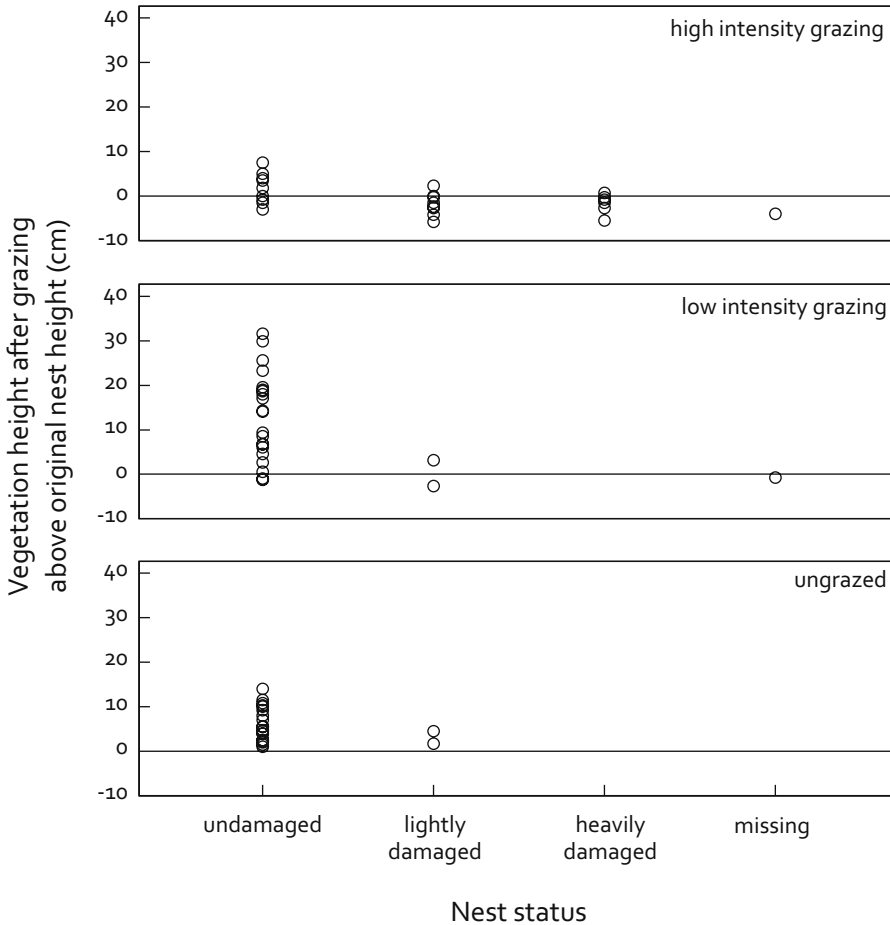


Figure 3. Vegetation height after the first grazing round (October) relative to the nest height prior to grazing, per nest status and grazing treatment.

Nest size as a proxy for caterpillar count

Nest volume in August was strongly correlated to the number of caterpillars per nest (Figure 4, Pearson correlation, $r = 0.79$, $n = 25$, $p < 0.001$). There was no difference in caterpillar density (number of caterpillars per nest volume) between the two study sites (t-test, $T_{23} = -0.69$, $p = 0.50$). This confirmed our assumption that nest volume could be used as a proxy for the number of caterpillars per nest.

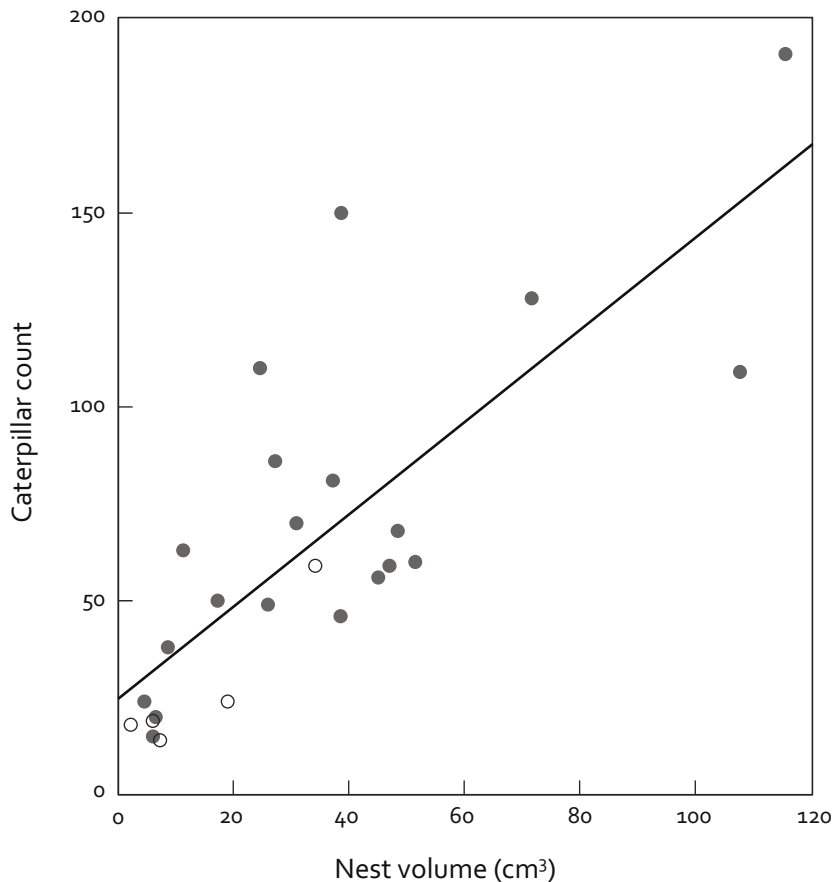


Figure 4. Relationship between nest volume and the number of caterpillars per nest in August ($R^2 = 0.62$) at Bemelerberg (high intensity grazing and no grazing treatment, represented by solid circles) and Thier de Lanaye (low intensity grazing, represented by open circles).

Nest volume

Prior to grazing, the nests at Thier de Lanaye (low intensity grazing treatment: mean nest size $14.0 (\pm 1.4 \text{ SE}) \text{ cm}^3$) were significantly smaller (t-test, $T_{72} = 12.4$, $p < 0.001$, critical $p = 0.017$) than at Bemelerberg (ungrazed treatment: mean nest size $59.6 (\pm 5.9 \text{ SE}) \text{ cm}^3$, heavily grazed treatment: mean nest size $59.9 (\pm 5.9 \text{ SE}) \text{ cm}^3$). At Bemelerberg, nest volume did not differ prior to grazing between the ungrazed and high intensity grazing treatment (t-test, $T_{47} = -0.03$, $p = 0.98$). During both grazing rounds nest volume declined strongly in all treatments (t-test, after first grazing round $T_{73} = -18.7$, $p < 0.001$, after second grazing round $T_{73} = -10.0$, $p < 0.001$). The relative decline in nest size during the first grazing round was stronger in the high intensity grazing treatment (81%) than in the ungrazed (61%) and low intensity grazing treatment (60%) (Table 3). Overall, nests that appeared damaged after the first grazing round decreased significantly more in size than undamaged nests (Figure 5, Mann-Whitney, $U = 248$,

Table 3. ANOVA results testing for differences between the grazing treatments with respect to change in nest volume after the first and second grazing round.

	F	df	p
After first grazing round (October)	11.026	2, 71	<0.001
No grazing - Low intensity			0.987
No grazing - High intensity			<0.001
Low intensity - High intensity			<0.001
After second grazing round (December)	1.057	2, 71	0.353
No grazing - Low intensity			0.998
No grazing - High intensity			0.445
Low intensity - High intensity			0.405

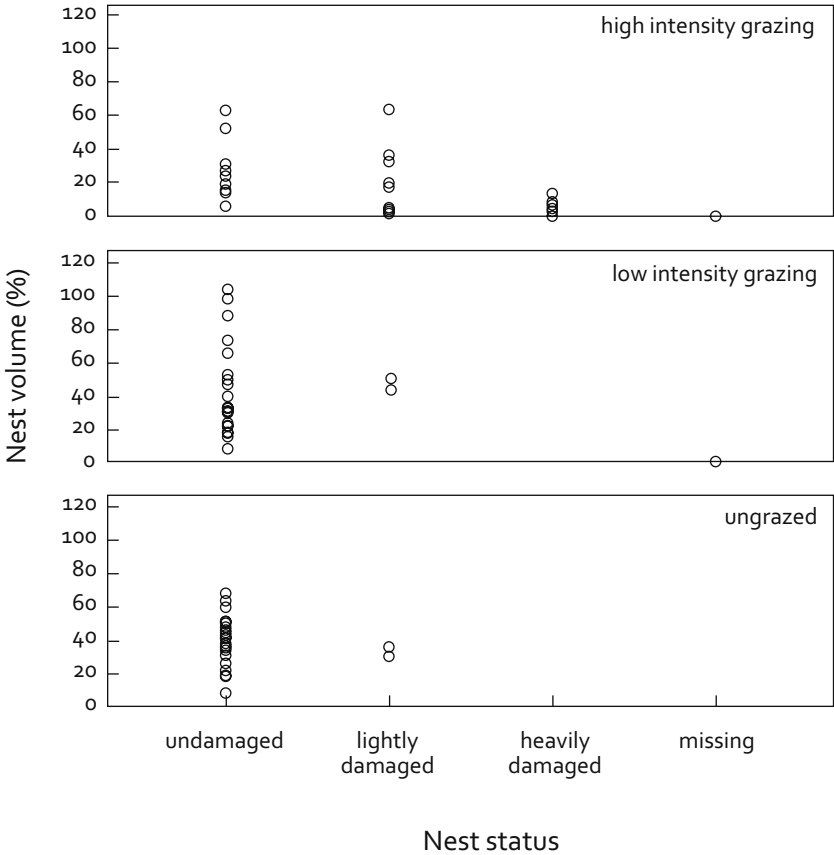


Figure 5. Nest volume after the first grazing round (October) as a percentage of the nest volume prior to grazing in relation to nest status.

$Z = 3.7$, $p < 0.001$). During the second grazing round the decline in nest size did not differ between treatments.

Spring caterpillar counts

As the nest size prior to grazing was significantly lower at Thier de Lanaye, absolute caterpillar counts in spring could not be used to assess the effects of grazing on caterpillar survival. Instead, we used the number of caterpillars per nest in early spring, relative to the nest size prior to grazing. This relative caterpillar count differed strongly between treatments (ANOVA $F_{2,71} = 10.8$, $p < 0.001$) with 50% lower caterpillar survival rates at the high intensity grazing treatment compared to both the ungrazed and the low intensity grazing treatment (Figure 6). Nests that appeared damaged after the first grazing round had significantly lower caterpillar survival rates than undamaged nests (Mann-Whitney, $U = 241$, $Z = -3.8$, $p < 0.001$).

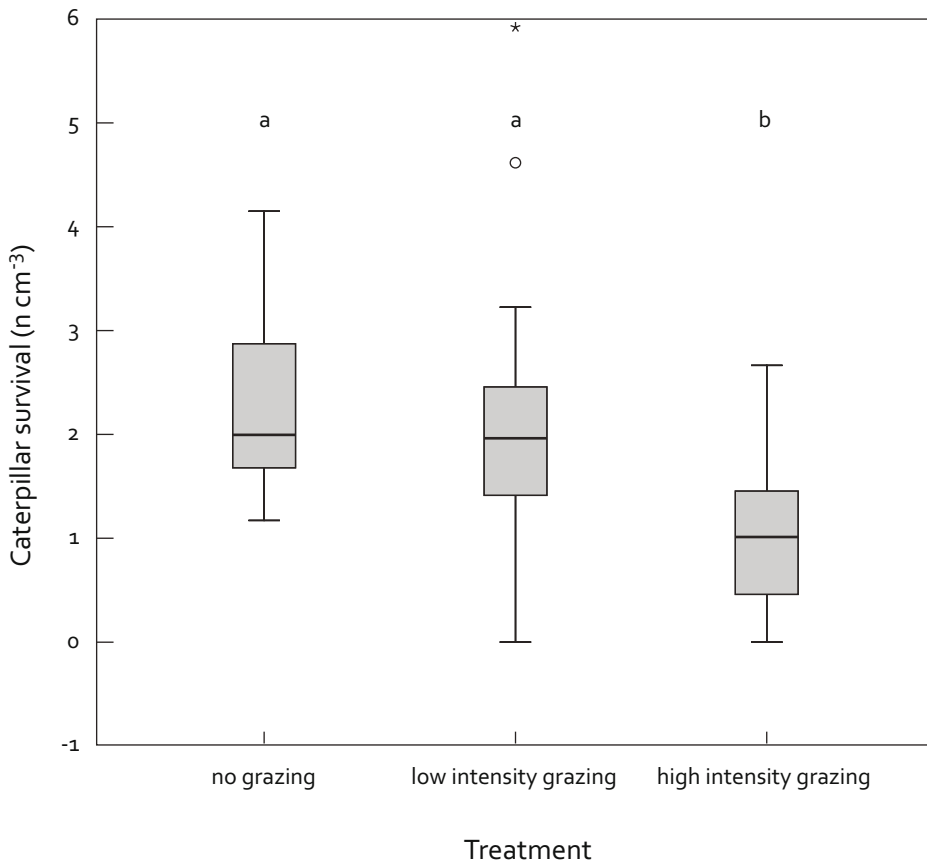


Figure 6. Boxplot showing caterpillar survival per treatment measured as the number of caterpillars in March relative to the nest volume prior to grazing (September). Different letters represent differences between treatments (significant at the 0.01 level). Symbols depict outliers (°) and extremes (*).

Discussion

Grazing is an essential management tool for the conservation of species-rich semi-natural grasslands (Baldock et al. 1996; Ostermann 1998; Willems 2001). However, grazing can also have severe negative effects on the very species the grazing management aims to conserve (Schtickzelle et al. 2007a; Konvicka et al. 2008). In this study we show that intensive sheep grazing can cause substantial damage to nests of hibernating *M. cinxia* caterpillars. Survival in the high intensity grazing treatment was about 50% lower than in the ungrazed treatment. We also provide evidence that grazing intensity can be an important factor determining the extent to which caterpillar nests are negatively affected by sheep grazing.

Effects of high intensity grazing

The decreased caterpillar survival rate in the high intensity grazing treatment was predominantly caused by a decrease in the number of surviving caterpillars per nest, rather than disappearance of whole nests. Nest survival was only slightly lower in the high intensity grazing treatment (88%), compared to the ungrazed control treatment (100%). Overall, nest survival in this experiment was extremely high, with nest survival rates in all treatments well above the 80% average overwinter nest survival reported for this species (Kuussaari 1998). In spite of the high nest survival rates, caterpillar survival was halved in the high intensity grazing treatment compared to the ungrazed control treatment. The number of caterpillars surviving per nest was especially low in nests that were heavily damaged. Some of the damaged nests (20%) were on the ground and looked flattened, suggesting that they were trampled. Most damaged nests however, were still suspended in the vegetation. The stronger reduction in vegetation height at damaged nest sites compared to undamaged nest locations, suggests that most nest damage was caused by sheep during grazing. Most likely the sheep ingested (partial) nests, tearing the silk and sometimes causing remaining caterpillars to fall out of the nest. This was confirmed by the fact that the vegetation height at damaged nest sites had on average been reduced to below the height where the nest had been prior to grazing. This means that the vegetation to which damaged nests were attached was in most cases eaten by the sheep, making it likely that the sheep ingested (partial) nests with this vegetation. In contrast, at undamaged nest sites the vegetation height after grazing was on average still higher than the nest height prior to grazing. Such ingestion of insects by grazers is known as incidental omnivory (Bonal and Munoz 2007; Gomez and Gonzalez-Megias 2002; Polis et al. 1989). For butterflies our study seems to be the first direct proof of such incidental omnivory, although it has previously been suggested to be a major cause of butterfly declines at grazed sites (Baines et al. 1994).

Interactions with habitat characteristics

In the low intensity grazing treatment, the impact of grazing on nest size and caterpillar survival was much lower than in the high intensity grazing treatment (no significant difference compared to no grazing). Nonetheless, the type of damage to caterpillar nests (trampling versus ingestion and the reduction in nest size per nest damage category) was similar at both study sites. This was unaffected by some apparent differences between

the two sites, like the average nest size prior to grazing, which was about four times larger at the high intensity grazing site. This indicates that the extent of damage to caterpillar nests, rather than the type of damage caused by grazing, varies under different grazing intensities.

Grazing intensity, habitat characteristics and herbivore behaviour are all likely to be major factors determining grazing impact on larval mortality. This is illustrated in our study by the absence of clear grazing effects (both on the vegetation and on caterpillar nests) after the second grazing round in the high intensity grazing treatment. This grazing round was conducted over a longer period and at much lower stocking densities than the first grazing round. Numerical grazing intensity (sheep-days $\cdot$ ha⁻¹) was higher than during the first grazing round in the low intensity grazing treatment, but apparently the experienced grazing pressure (i.e. the proportion of vegetation removed close to caterpillar nests) and hence actual nest damage were much lower. Also, nest survival rates in both grazed treatments in this study were considerably higher than the survival rates measured during a pilot study in 2007. In this pilot, conducted at the same sites and with the same experimental set-up, only two out of seven nests (30%) survived in the high intensity grazing treatment, compared to five out of seven (70%) in the low intensity grazing treatment and seven out of seven (100%) in the ungrazed control (C.G.E. van Noordwijk, unpublished data). It thus appears that the effect of grazing on nest survival may vary substantially between years, as was previously reported for incidental omnivory on phytophagous beetles (Bonal and Munoz 2007; Gomez and Gonzalez-Megias 2002). This variation may be due to the fact that the proportion of removed vegetation does not only depend on grazer density, but also on the amount and quality of food available to the grazers (Prache et al. 1998; Roguet et al. 1998). Food availability may vary substantially between years, depending on weather conditions (driving biomass production) and availability of alternative food sources. Grazing impact is also likely to show spatial variation within the site (Prache et al. 1998). In addition, weather conditions in the period preceding or following management may also alter the effects of grazing, through shifts in the importance of food or shelter availability for insects. This has been reported as a cause of major variation in insect mortality caused by mowing (Humbert et al. 2009). More elaborate replicated studies are highly needed to establish more exactly how grazing intensity influences larval survival and how this interacts with habitat characteristics and grazing behaviour.

Species-specific traits affecting vulnerability to grazing

It is increasingly acknowledged that the extent to which different species are affected by particular disturbances can be predicted from their traits (Berg et al. 2010; Van Kleef et al. 2006; Van Turnhout et al. 2010; Vandewalle et al. 2010; chapter 3). There are a number of traits that determine the vulnerability of invertebrate species to grazing management and especially incidental omnivory. First, sedentary species are more severely affected than mobile arthropods. Mobile species may be able to evade grazers by flying or walking away (Berggren 2004) or simply dropping to the ground (Gish et al. 2011). In contrast, species living within plant structures will be unable to evade grazers (Gomez and Gonzalez-Megias 2007) as will inactive insects (e.g. hibernating) and insects

living within closed cocoons or silk nests. Also, mobile species can only evade grazers if they can detect them in time (Gish et al. 2010; Gish et al. 2011).

A third characteristic affecting species' vulnerability to grazing management is their location within the vegetation, especially during immobile life stages. Many grazers, including sheep, graze selectively (Parsons and Dumont 2003; Roguet et al. 1998), favouring highly palatable items like flowers, buds and forbs over food items with low nutritional value, like tall grasses. Invertebrates associated with the favoured vegetation structures are therefore likely to be more affected by grazing management, even at relatively low grazing intensities. In addition, invertebrates living higher in the vegetation column will have a higher risk of incidental omnivory than species living close to the ground (Zamora and Gomez 1993).

Body size is another life-history trait that possibly affects a species' risk to incidental omnivory. Mowing has been demonstrated to be more detrimental to large-bodied species than to small species (Humbert et al. 2010; Humbert et al. 2009). To what extent this also applies to mortality caused by grazing is unclear. In contrast to mowing, grazers may actively avoid insects depending on their ability to detect them. Large-bodied species will generally have a higher chance of being detected by the grazer than small species. On the other hand, just as with mowing, larger species, or structures such as caterpillar nests, have a higher chance of being encountered purely by chance. While individual species are likely to die even when only a part of them is ingested, this is not the case for clusters of individuals, like a caterpillar nest of *M. cinxia*. Our results confirm that for such gregarious species, damage to the nest due to incidental ingestion does not necessarily lead to mortality of the whole larval group. This reduces the negative effects of increased encounter rates of larger species and renders it likely that the effects we found are similar for caterpillars hibernating individually.

Timing of grazing

The identified traits determining a species' vulnerability to incidental omnivory vary throughout the life-cycle of most invertebrate species, including butterflies. This means that the impact of grazing management strongly depends on the timing of this management in relation to the phenology of the species. Most butterflies living in temperate grasslands are inactive during the winter months, often hibernating as immature stages. Previous studies have often recommended to confine grazing and mowing management to this inactive winter season (Ellis 2003; Oates 1995; Schtickzelle et al. 2007a) to minimise negative effects on food and oviposition site availability. However, our results show that this advice may have serious consequences for larval survival. In Dutch calcareous grasslands, where introduction of autumn grazing around 1980, led to improved habitat conditions for most calcareous grassland butterflies (Smits 2010), these species did not recover. Remaining populations of *Erynnis tages* and *Aricia agestis* even continued to decline and other species, which had already disappeared, did not return (WallisDeVries et al. 2002). All these species hibernate as inactive caterpillars or pupae in the vegetation or litter layer of nutrient-poor grasslands (Bink 1992). Our results suggest that the management aimed at the conservation of these threatened species and restoration of their habitat may have had adverse consequences. Similarly, Smee et al. (2011) have

demonstrated that the occurrence of the endangered *Euphydryas aurinia* (Annex II species of the European Habitats Directive) in the UK was especially determined by high sward heights in autumn, in addition to food plant availability and intermediate stocking density. The life-cycle of *E. aurinia* closely resembles that of *M. cinxia*, which renders it very likely that incidental ingestion is also a large threat for this highly endangered butterfly species. Based on our results, we thus strongly oppose the advice to confine grazing and mowing management to the inactive winter season. In general, we expect that mortality rates will be much lower when management is conducted while species are active (not hibernating). Also, adult life-stages are generally more mobile and less demanding with respect to their habitat requirements than immature stages (Bourn and Thomas 2002; Fartmann and Hermann 2006), making them less vulnerable to negative effects of management practises.

Implications for conservation management

This study illustrates the need to strike the balance between positive and negative effects of management measures, in order to integrate the requirements of different organisms (WallisDeVries et al. 2002) and life-stages in semi-natural grassland conservation. Balancing positive and negative effects of management for a large range of species, including plants and animals, is not an easy task. Management in semi-natural grasslands should be intensive enough to reduce nutrient availability (Willems 2001) and to create a heterogeneous vegetation structure with favourable microclimatic conditions for plants (Bobbink and Willems 1993) and invertebrates (Morris 2000; Morris et al. 1990; Poyry et al. 2004). At the same time disturbance should be kept to a minimum. This delicate balance is compromised even more as intensive management is currently needed to overcome the encroachment of coarse grasses and shrubs due to abandonment (EEA, 2004; Laiolo et al., 2004), increased nitrogen deposition (Bobbink and Hettelingh 2011; Bobbink et al. 1998) and climate change (WallisDeVries and Van Swaay 2006). At the same time land-use change has caused increased habitat fragmentation, which negatively affects the ability of populations to recover from local disturbances (Hodgson et al. 2005; Kruess and Tscharntke 1994). To minimise damage to endangered insect populations the management regime should be tailor-made to suit the needs of locally occurring species, while being adapted to the local vegetation productivity. Effects of management measures on species can be predicted from their traits (life-history and behavioural). Incorporating species traits in the design of habitat management plans thus appears a prerequisite for success, but this approach has not yet been widely applied (Verberk et al. 2008b; chapter 3). Our results demonstrate both the need to start incorporating these traits in conservation policy and practice as well as the necessity to pay more attention to inactive and immature life-stages. In particular, agri-environment schemes for semi-natural grasslands and conservation action plans for endangered butterflies, such as the European habitats directive species *Euphydryas aurinia*, should incorporate the effects of high intensity autumn grazing on hibernating caterpillars.

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Appendix 1. Photos of caterpillar nests



Figure A1. Several caterpillar nests (white blotches) in a calcareous grassland vegetation in summer (Photo C.G.E. van Noordwijk August 2011).



Figure A2. Close up of a *Melitaea cinxia* caterpillar nest in summer (Photo D.E. Flierman August 2009).



Figure A3 & A4. Undamaged caterpillar nest after grazing (Photos D.E. Flierman October 2009)



Figure A5 & A6. Lightly damaged caterpillar nest after grazing. The silk is clearly damaged, but the caterpillars remain inside the nest (Photos D.E. Flierman October 2009).



Figure A7 & A8. Heavily damaged caterpillar nest after grazing. The silk nest is heavily damaged and no longer seems to contain any caterpillars. Some caterpillars can be seen on the ground (Photos D.E. Flierman October 2009).

Heavily damaged common blue (*Polyommatus icarus*) after hay cutting (Photo: Toos van Noordwijk)



Chapter 6

A multi-generation perspective on functional connectivity for arthropods in fragmented landscapes

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Abstract

Functional connectivity depends on landscape structure and species' dispersal behaviour and it affects species persistence in fragmented landscapes, especially under climate change. Species persistence also depends on demographic vital rates, but insight into the relative importance of these three groups of parameters for the spread of species in a fragmented landscape is limited. In this paper we used an individual-based and spatially-explicit model of arthropods in Dutch calcareous landscapes, to determine to what extent landscape structure, species' dispersal behaviour and demographic vital rates influence a species' spread rate in fragmented landscapes. In addition, we explored whether different landscapes favour different dispersal traits and vital rates and whether such interactions lead to different rank orders of potential restoration strategies for different arthropod species.

All main effects and two-way interactions of the included parameters explained 93-99% of the variance in four response variables representing aspects of spread and population density. Most variance (39-79%) was explained by dispersal behaviour, but landscape structure and demography still explained 10-38% and 5-18% of the variance, respectively. Interactions between landscape attributes and species properties (dispersal traits and vital rates) in total explained less than 5% of variance. The absolute effects of restoration measures differed markedly between species groups, but the ranking order of the effects of restoration scenarios on spread and species persistence were similar across species. Strongest improvements in population density and maximum distance reached were found for increased habitat availability, while effects of increased habitat clustering and improved matrix quality were generally limited.

These findings show that dispersal, landscape and demography parameters all affect species persistence and spread in fragmented landscapes, which highlights the need to incorporate all three parameter categories when studying species' spread rates. In addition, our study indicates that even under a ten-fold increase in available habitat, some arthropod species may only spread over a few hundred metres in 10 years. This suggests that species persistence under climate change may be best protected by creating large heterogeneous habitats with a range of microclimatic conditions, rather than relying on species to keep up with shifting climate envelopes.

Introduction

Landscape connectivity, defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor 1993), is a key concept in spatial ecology. It is influenced both by attributes of the landscape and by behaviour of the species in it (With et al. 1997; Baguette and Van Dyck 2007). Studies incorporating the interplay between these two often use the term functional connectivity (With et al. 1997; Bowler and Benton 2005; Baguette and Van Dyck 2007), as opposed to structural connectivity, which refers to the effect of landscape attributes *per se*. Functional connectivity has profound effects on biodiversity conservation (Hastings 1980; Tilman et al. 1994; Benton et al. 2002), as long-term species persistence is affected by the ability of species to disperse between habitat patches (Fahrig and Merriam 1985; Hanski 1999). This is especially true in highly fragmented landscapes, where small populations have an increased chance of local extinction (MacArthur and Wilson 1967; Dorp and Opdam 1987; Hanski 1999). In recent decades climate change has added further importance to functional connectivity (Opdam and Wascher 2004; Hodgson et al. 2009). The occurrence of extreme weather conditions is increasing (IPCC 2007). As a consequence, local population extinctions become more frequent (Opdam and Wascher 2004; Thomas et al. 2004), making the ability to recolonise empty habitat patches crucial for species persistence. In addition, formerly suitable habitat patches may become unsuitable under climate change, forcing species to shift their distribution range (Walther et al. 2002). Effective biodiversity conservation in fragmented landscapes therefore requires thorough understanding of the factors affecting functional connectivity.

Important landscape factors governing functional connectivity include the amount of available habitat and its spatial configuration (Hanski 1999) as well as the quality of the interspersing matrix (Baum et al. 2004; Prevedello and Vieira 2010). From the species' perspective, a range of traits and behavioural responses (here collectively referred to as dispersal traits) govern the three stages of the dispersal process: departure, inter-patch movement (transfer) and settlement (Isard and Gage 2001; Bowler and Benton 2005). These dispersal traits include, amongst others, movement ability, dispersal mortality, behavioural responses to boundaries and perceptual range (Bowler and Benton 2005). While our knowledge of dispersal traits and landscape attributes that affect functional connectivity is growing, our understanding of how they interact to form observed patterns at the community level is still limited.

In addition, island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski 1999) highlight that population persistence in spatially structured systems is also strongly affected by demographic vital rates (resulting in variability in reproductive output and population size). Indeed, demographic details are increasingly incorporated in spatial dispersal models (see Jongejans et al. 2008 for an overview). However, while these studies explore the effect of vital rates on functional connectivity, the process of dispersal itself has either been collapsed into a single dispersal parameter (dispersal kernel) or is only dealt with implicitly through altering colonization and extinction rates. This excludes any underlying aspect of the species' dispersal ecology (Travis et al. 2012). Modelling studies incorporating detailed movement rules across species on the other hand have been limited to the study of individual movements within a single generation (Pe'er et al. 2011),

so neglecting any demographic component of the spread proces. To accurately predict biodiversity loss in fragmented landscapes or the effectiveness of proposed conservation measures, spread processes should be studied over several generations, incorporating population dynamics in these models (Jongejans et al. 2008).

In this paper we present such an approach, building further on an earlier developed individual-based dispersal model (Bonte et al. 2010) to infer population spread in fragmented landscapes over 10-100 generations. As a case study, we parameterized the model to represent arthropods in Dutch calcareous grasslands. This case study was chosen because it represents a highly fragmented system (around 1% calcareous grassland habitat) that is potentially very species-rich (WallisDeVries et al. 2002). The inhabiting arthropod species cover a wide range of values for dispersal traits and vital rates. Moreover, habitat isolation and fragmentation have been identified as major bottlenecks hampering biodiversity conservation in this system (chapter 3). Our first aim is to establish the relative importance of demographic vital rates, dispersal traits and landscape structure for functional connectivity. We do this by means of a fully factorial dataset containing several parameters for each category of traits and attributes. Secondly, we investigate how species' dispersal traits and vital rates interact with landscape attributes. King and With (2002) demonstrated for simple movement algorithms that dispersal behaviour only affects dispersal success below specific habitat availability thresholds. Above this threshold all species are able to disperse through the landscape, even if they are relatively poor dispersers. Theoretically it can be expected that there is also a lower threshold, below which all species are unable to disperse through the landscape even if they are good dispersers. In addition, different landscape structures may favour different trait attributes (Schtickzelle and Mennechez 2006; Merckx and Van Dyck 2007). Thirdly, we investigate whether the interactions between dispersal traits, vital rates and landscape attributes lead to different restoration strategies being most effective for different arthropod species. Several conservation measures can be taken to counter decreased structural connectivity, including increase of habitat availability, increase of habitat contagiousness (creating more connected sites) and increase of matrix quality. There has been heated debate over which strategy is most effective (Hodgson et al. 2009, 2011a; Doerr et al. 2011). However, if the effectiveness of different restoration strategies depends on dispersal traits and vital rates, there may not be a single most effective strategy for all species collectively. Moreover, previous studies have shown that restoration strategies that promote dispersal, frequently are not the most optimal strategies for species persistence (Hodgson et al. 2011b, 2012). To address this issue we study the effect of restoration scenarios both on dispersal distances and on total population densities.

Methods

Model description

Study system

We developed a continuous time, spatially explicit, individual-based model for simulating the movement and population demography of species inhabiting fragmented landscapes. Here, we used this model to simulate the spread of species according to variation in vital rates, movement behaviour and landscape structure. We parameterized the model to represent arthropods in Dutch calcareous grasslands. Landscape parameters were based on the landscape of South-Limburg (50° 51' N, 5° 52' E, altitude 50-150 m above sea level), which represents a potentially very species-rich, but highly fragmented system. Vital rates and movement behaviour parameters were based on realistic values for (female) arthropods. As an exception, values for the carrying capacity (K) were downscaled to reduce model runtime. The model was run for 1000 time steps, with each time-step representing 1 day. Assuming that simulated arthropods have an active period of 100 days per year, this represents a period of 10 years.

Landscape

We ran simulations in binary, fractal landscapes with low (<10%) habitat availability. This black-and-white representation of the landscape consisting of suitable habitat and hostile matrix is clearly an oversimplification of reality for most species, but can be considered representative for specialist calcareous grassland arthropods in landscapes dominated by intensive agriculture (chapter 7). We tested our hypotheses using replicated, relevantly fragmented landscapes by varying the amount of habitat (P) and the level of spatial contagion (H). These landscapes were generated using the mid-displacement diamond algorithm (Gardner and Urban 2007) and had a dimension of 128×128 grid cells. They are referred to as neutral landscapes and can be independently replicated based solely on the P and H parameter values. The parameters were scaled such that each grid cell represented 1 hectare, causing the landscape as a whole to represent 12.8×12.8 km with the grain size of the habitat being 1 hectare. Individuals moved within the landscape in a continuous way at a scale of 1/100 of the grid cell resolution, corresponding to a unit of movement of 1 meter. We followed the spread of a population from one side of the landscape (south) to the upper part (north). Connectivity was considered successful if the population colonized habitat at the upper part of the landscape (upper 28 grid cells) within 1000 time steps. The upper and lower boundaries were absorbing; those at the sides were wrapped.

Individuals

All individuals carry information that is either individually fixed (age at maturity, baseline mortality, maximal reproductive effort) or dynamic ($[x,y]$ position in meters, movement angle, age, time in matrix). Other information is fixed at the population-level, i.e. equal for all individuals within the simulation and considered as a species-specific property (maximal speed, speed increase in the matrix, perceptual range and carrying capacity). An overview of the simulated traits and attributes is provided in Table 1.

Table 1. Parameter values used for the full analysis. Abbreviations used in the text, other than the symbols used in equations, are given between brackets.

Category	Parameter	Symbol	Fixed value over all simulations	Scenario settings
Landscape	Proportion of suitable habitat	P		0.01, 0.05, 0.10
	Fractal dimension (level of autocorrelation)	H		0.1, 0.3, 0.5
Vital rates	Age at maturity in t units	AAM		10, 50, 100
	Standard deviation of AAM	SD(AAM)	0.3	
	Spatial extent of the density dependent processes	DDP	10	
	Carrying capacity	K		2, 5
	Maximum growth rate	r	Set to K	
	Environmental stochasticity, in proportion to r	σ	0.2	
	Aging mortality	μ_{aging}	0.005	
	Baseline mortality	μ_{base}	0.001	
Dispersal traits	Maximal step length per time unit (maxspeed)	Lmax		5, 50, 500
	Speed increase factor in matrix (speedfact)	SIF		1, 10, 100
	Transfer mortality (mudisp)	μ_{isp}		0.1, 0.3, 0.5
	Patch emigration probability	Pcross		0.1, 0.5, 0.9
	Directionality deviance factor	DF	5	
	Perceptual range in grid cell units (percrange)	n		0, 1, 10
	Time frame of neglecting borders after emigration	γ	10	

Population dynamics

Population dynamics were modelled by means of a stochastic individual-based formulation of logistic growth. At the time of reproduction (age at maturity), each individual has a mean reproductive output

$$\Lambda \sim \text{Poisson}\left(\frac{r}{N}\right)$$

With r the basic growth rate and N the density of individuals within the grid cell. In all simulations r was set to equal K , thus assuming that offspring of one individual are able to settle into one grid cell. The effective number of offspring λ is drawn from a $N(\Lambda, \sigma)$ with Λ the previously defined species-specific mean reproductive output and σ the amount of experienced demographic stochasticity. Reproduction takes place when an individual is in suitable habitat. After reproduction, the individual dies.

Before reproduction, individuals face two sources of mortality: aging μ_{aging} and dispersal costs μ_{disp} during the transfer phase in the matrix. These two mortality rates are per step probability functions in function of the predefined baseline mortality μ_{base} .

$$P(\text{aging mortality}) = \mu_{base}^{(\mu_{aging} * \text{age})} \quad \text{and}$$

$$P(\text{transfer mortality}) = \mu_{base}^{(\mu_{disp} * \text{time in matrix})}$$

Movement dynamics

Individual movement was modelled by simulating positions at each time step t based on step-length ϑ and movement angle Θ such that: $x_t = x_{t-1} + \vartheta \cos \Theta$ and $y_t = y_{t-1} + \vartheta \sin \Theta$, which can be easily combined in a tangens rule. With step length at each time step t : $\vartheta \sim \text{Poisson}(L)$ and L drawn from a uniform distribution $[0-L_{max}]$. Movements within habitat followed a Brownian motion according to ϑ and random movement angles Θ . The movement rules explicitly follow the different behavioural rules of the emigration, transfer and immigration phases of dispersal (Travis et al. 2012):

Departure: from the moment an individual crosses the boundary between suitable habitat and matrix, it crosses the border with a probability P_{cross} , otherwise it continues random movement within the habitat. We consider emigrants to be in a dispersal phase and therefore not using any perceptual ability to detect suitable habitat within the first n time steps after crossing the border. The number of time steps individuals neglect their perceptual range (n) is $\text{Poisson}(\gamma)$, with γ a predefined time frame of non-informed movement.

Transfer: we modelled movement during transfer to be faster than within habitat movement by multiplying step length ϑ with a predefined speed increase factor (SIF). Movements during transfer are more directional (see e.g. Van Dyck and Baguette 2005), which we modelled by reducing the additive angle deviance: $\Theta_{t+1} = \Theta_t + \eta$ with $\eta = \Theta_{t+1} * \text{rnd}[-0.5 \dots 0.5] / DF$. DF is a predefined fixed deviance factor.

Settlement: moving individuals enter suitable habitat when the border between habitat and matrix is crossed during movement. Individuals are attracted to suitable habitat within their perceptual range. Movements are directional with a new movement angle with the probability of choosing a new angle in the direction of the attractor being relative to the proportion of suitable habitat within that sector. Step lengths are identical to those obtained during the transfer phase. Because the new direction is determined according to the total available habitat within the four distinguished sectors, shadow effects are overcome, and information use is area rather than perimeter scaled (see Englund and Hambäck 2007).

Simulations and analyses

Basic simulations

We ran a fully factorial set of simulations with varying values for each of the landscape-, vital rate- and movement behaviour parameters outlined in Table 1. Each parameter combination was replicated five times through the use of five randomly generated landscapes for each combination of P and H (see above). The output was given as the number of individuals per grid cell layer (row of grid cells from south to north) after 1000 time steps (spatial output) and as the total number of individuals in the target area (northern most 28 grid cells) at each time-step (temporal output). From these we calculated four response variables for each simulation:

extinction: whether the population has gone extinct (0/1);

reached other side: whether at least 1 individual has reached the target area at any one time and the population has not gone extinct (0/1);

population density: total number of individuals in the landscape after 1000 time steps;

arrival time: time step at which the first individual entered the target area.

For all four response variables we used GLMM analyses to determine how much variance is explained by each parameter, using the `lmer` function in R (R Core Development Team 2013) package `lme4` (Bates et al. 2013). All main effects and two-way interactions of parameters were included as random variables as we were primarily interested in the proportion of variance explained by each of them. For the response variables extinction and reached other side we used a binomial distribution. The response variables population density and arrival time were natural log transformed to satisfy a normal distribution.

Conservation scenarios

From the above simulations we selected 20 parameter combinations to represent a baseline landscape and four different restoration scenarios, each for four groups of species (see Table 2). The baseline landscape had 1% habitat (P) and a spatial contagion level (H) of 0.1. As restoration scenarios we compared a five- and tenfold increase in available habitat without increasing the level of spatial contagion (scenarios 5-fold fragmented and 10-fold fragmented), a fivefold increase in available habitat accompanied by decreased fragmentation through an increase in the spatial contagion to 0.5 (scenario 5-fold clustered) and an increase in matrix quality, simulated by decreasing dispersal mortality by 0.2 (scenario Matrix quality). For the vital rate- and movement behaviour parameters we chose four combinations which together represent a large proportion of typical calcareous grassland arthropods, including walking and flying species with low and high population densities and varying levels of border-crossing behaviour. Parameter choices were based on literature sources for a wide range of arthropod species (Bink 1992; Kleukers et al. 1997; Gutiérrez et al. 1999; Maes et al. 2006; Seifert 2007) and for each group an example species is listed in table 2. As response variables, we compared total population density after 1000 time steps and maximum grid cell line (measured from the bottom) inhabited after 1000 time steps.

Table 2. Parameter values used for the restoration scenarios. For each species group one example is given of a real calcareous grassland arthropod species, with the UK common name between brackets.

Species groups	Lmax <i>m/day</i>	SIF <i>factor</i>	Pcross <i>prob</i>	K <i>nr/ha.</i>	μ_{disp} <i>prob</i>	n <i>m</i>	AAM <i>days</i>
a) Flying-high pop. density - FH <i>Lasius alienus</i> (Ant – no UK common name)	50	10	0.9	5	0.5	10	100
b) Flying- low pop. density - FL <i>Erynnis tages</i> (Dingy Skipper)	50	10	0.1	2	0.3	10	100
c) Walking- high pop. density - WH <i>Tapinoma erraticum</i> (Erratic ant)	5	1	0.5	5	0.3	10	100
d) Walking- low pop. density - WL <i>Stenobothrus stigmaticus</i> (Lesser mottled grasshopper)	5	1	0.1	2	0.3	10	100
Landscapes	<i>P</i>		<i>H</i>		μ_{disp}		
Basic	0.01		0.1		base		
Matrix quality	0.01		0.1		-0.2		
5-fold fragmented	0.05		0.1		base		
5-fold connected	0.05		0.5		base		
10-fold fragmented	0.10		0.1		base		

Results

Relative importance of vital rates, dispersal traits and landscape structure

Analysis of the fully factorial dataset revealed that the main effects and two-way interactions of all included parameters explained between 93% and 99% of the variance for the four response variables. The largest residual variance (6.4%) was found for the response variable arrival time. For all four response variables, each of the three parameter categories (vital rates, dispersal traits and landscape structure) were included in the five most influential parameters (Figure 1; Appendix 1). Extinction chances, chances of reaching the other side and arrival time were most affected by dispersal behaviour (explaining 62-79% of the variance). However, landscape structure and population vital rates each still explained 10-28% and 5-8% of the variance respectively for these response variables. Population density was more strongly affected by landscape attributes (38% explained variance) and vital rates (18% explained variance) than the other response variables, with dispersal traits explaining 39% of the variance.

Within the range of implemented realistic landscape values, the amount of habitat (*P*) was always more influential than the spatial configuration of habitat (*H*). The most influential dispersal traits were dispersal mortality (*mudisp*), border crossing behaviour (*pcross*) and speed (both *maxspeed* and *speed factor*). The order of importance of

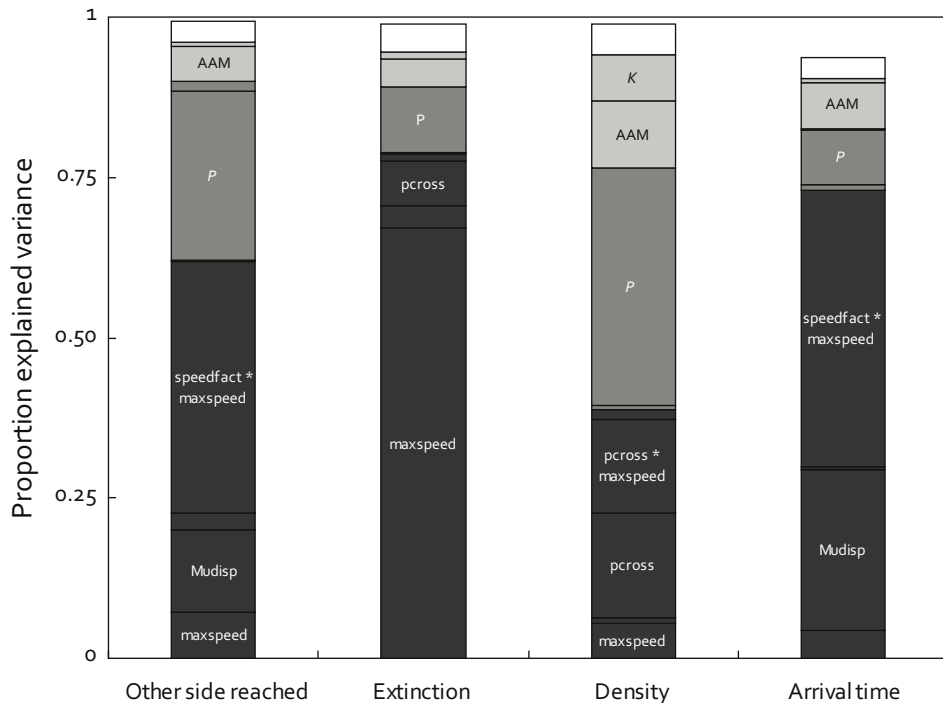


Figure 1. Proportion of variance explained by dispersal behaviour (black), landscape parameters (dark grey), vital rates (light grey) and interactions between these categories (white) for each of the four response variables: 1) whether the other side of the landscape is reached, 2) whether the population went extinct, 3) the total population density and 4) the time to first arrival. Labels are given for all parameters explaining more than 5% of the variance (see Table 1 for parameter abbreviations).

these traits differed between response variables. Only one dispersal trait was consistently unimportant: perceptual range, which explained less than 1% of variance, both alone and in interaction. Concerning the population vital rates, age at maturity (AAM) was more influential than population carrying capacity. The carrying capacity (K) most strongly affected the final population density (7.1% explained variance), but was less influential for the chance of extinction, the chance of dispersal and the duration to first arrival (<1.2% explained variance).

Interactions between landscape attributes and species properties

Interactions between landscape attributes and species properties (dispersal traits and population vital rates) explained some of the variance for all response variables, but never more than 5% in total. Most interactions arose because individuals were unable to disperse and survive in landscapes with a low proportion of habitat, irrespective of their traits or vital rates, while traits and vital rates did influence dispersal at higher levels of habitat availability (Figure 2). Only for border crossing behaviour we found that opposite trait values were beneficial in different landscapes. Arrival time was highest at low border crossing probabilities for landscapes with 10% habitat, while it was highest at high

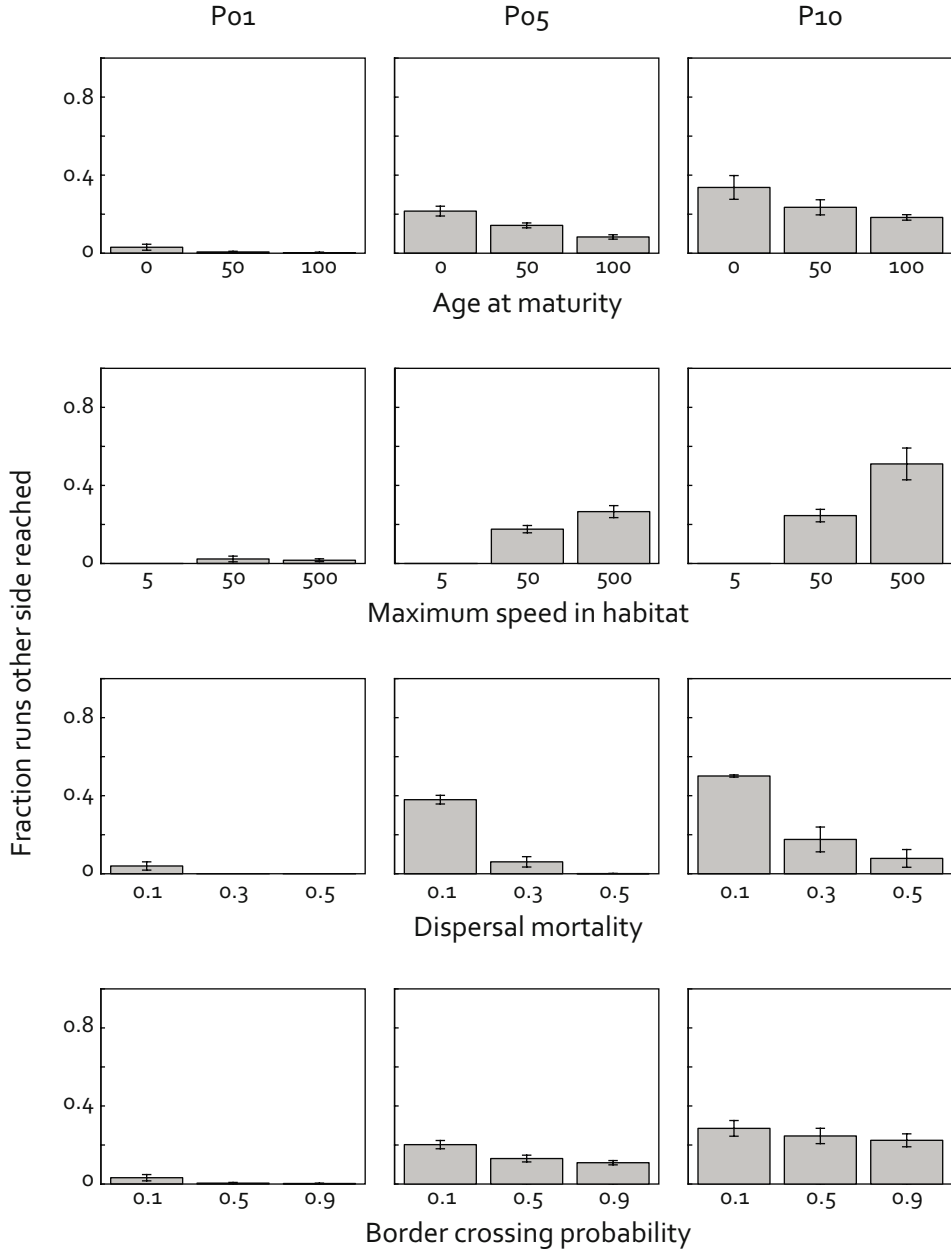


Figure 2. Fraction of runs with dispersal across the landscape within 10 simulated years depending on (from top to bottom) the maximum speed, dispersal mortality, age at maturity and border crossing probability for landscapes with 1% habitat (left), 5% habitat (middle) and 10% habitat (right) and H (the level of autocorrelation) set to 0.3. Error bars represent standard errors across the five replicate landscapes.

crossing probabilities in landscapes with 1% habitat (Figure 3). Total population density was however highest when individuals had low probabilities to leave habitat, irrespective of the amount of habitat in the landscape (see Figure 3).

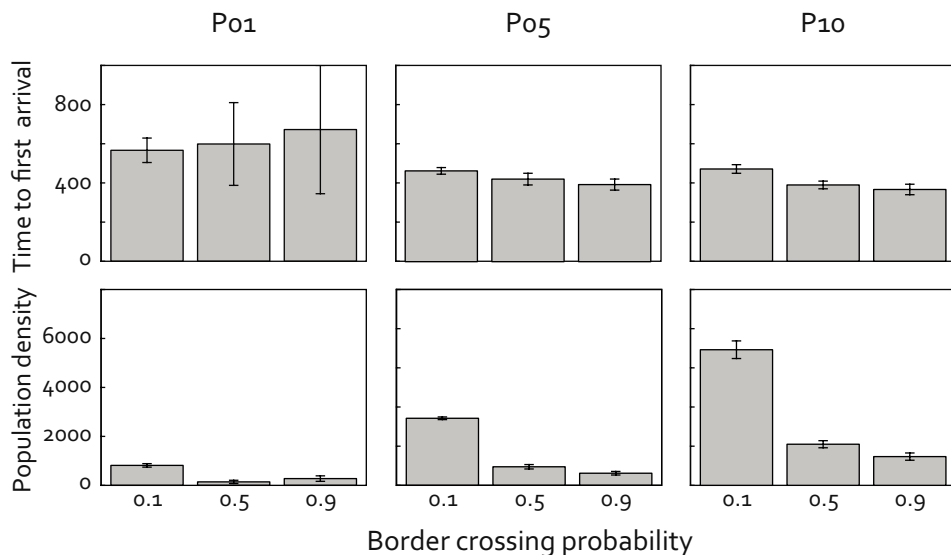


Figure 3. Mean duration to first arrival at the opposite side of the landscape (upper panels) depending on the border crossing probability (x-axis) in landscapes with 1% habitat (left), 5% habitat (middle) and 10% habitat (right) and H (the level of autocorrelation) set to 0.3. The lower panels show the population density after 10 years under the same conditions. Error bars represent standard errors across the five replicate landscapes.

Restoration scenarios

Analysis of the effect of four alternative restoration scenarios on population density revealed that responses were similar across the four selected species groups (Figure 4). Improving matrix quality had little effect on population density, while a ten-fold increase in available habitat was the most effective strategy for all four species groups. However, the difference between a ten-fold and a five-fold increase in available habitat was more pronounced for flying than for walking species. For three out of the four studied species groups, adding habitat in clusters (scenario 5-fold clustered) was more effective than adding habitat while maintaining low habitat contagion (scenario 5-fold fragmented). For the fourth group (FL) there was no difference in final population density between scenarios 5-fold fragmented and 5-fold clustered.

With regard to the maximum distance travelled through the landscape after 10 years, differences between the species groups were more pronounced (Figure 5). Restoration scenarios increased the maximum distance travelled with up to 6 or 10 km for flying species, while the increase realised by walking species was no more than 500 meters.

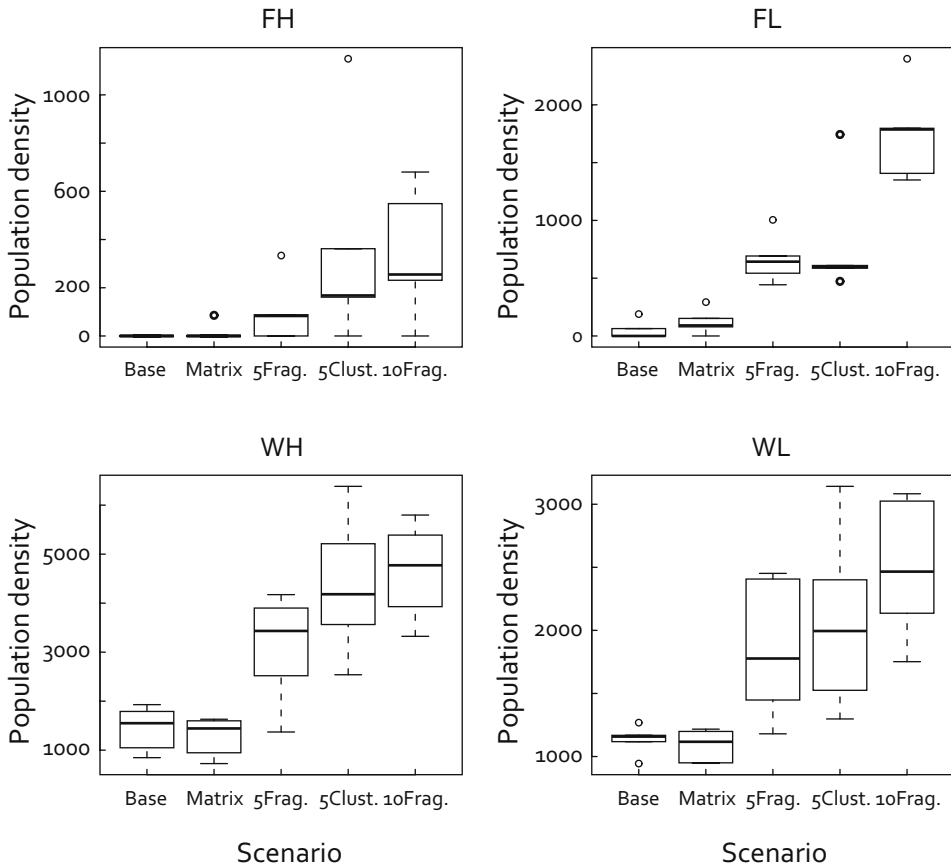


Figure 4. Population density after 10 years under different restoration scenarios (baseline, increased matrix quality, five-fold increase in habitat availability fragmented, five-fold increase in habitat availability clustered and ten-fold increase in habitat availability fragmented) for four different species groups, FH, FL, WH and WL (see Table 2 for landscape and species parameter settings).

Improving matrix quality was effective for species group FL, depending on the landscape (high variance). It had no effect for the other three species groups. For the two walking species groups there was no difference between a five-fold (5-fold fragmented) and a ten-fold (10-fold fragmented) increase in available habitat, while flying species dispersed further in the 10-fold fragmented scenario. Differences between scenarios 5-fold fragmented and 5-fold clustered were non-existent for species groups FH and WH and contrasting for groups FL and WL. Species group WL reached highest distances under scenario 5-fold clustered, while species group FL reached highest distances under scenario 5-fold fragmented.

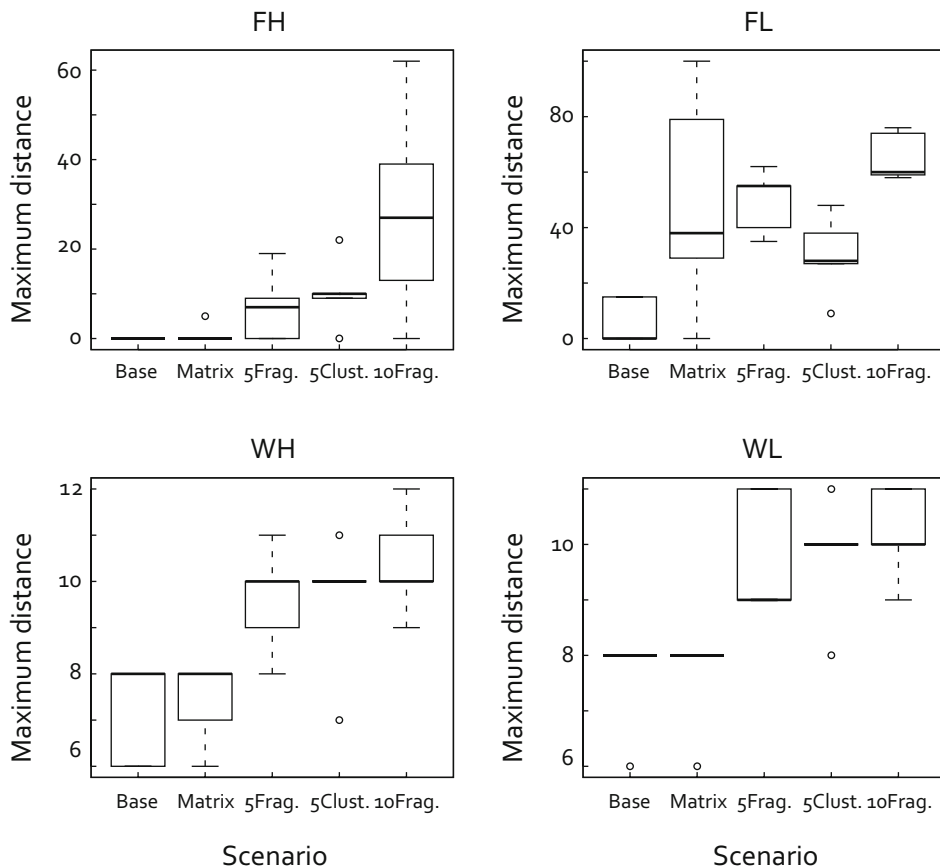


Figure 5. Maximum distance reached after 10 years under different restoration scenarios (baseline, increased matrix quality, five-fold increase in habitat availability fragmented, five-fold increase in habitat availability clustered and ten-fold increase in habitat availability fragmented) for four different species groups, FH, FL, WH and WL (see Table 2 for landscape and species parameter settings).

Discussion

Our results demonstrate that species persistence and dispersal in fragmented landscapes are governed by landscape structure, species' dispersal traits and their demographic vital rates. This is theoretically a logical consequence of combining classical island biogeography theory (MacArthur and Wilson 1967; Brown and Lomolino 2000) and movement ecology (e.g. King and With 2002; Bowler and Benton 2005; Baguette and Van Dyck 2007; Nathan et al. 2008). Indeed, the notion that all three abovementioned aspects affect functional connectivity has previously been recognised in both invasion ecology and conservation ecology (Neubert and Caswell 2000; Lockwood et al. 2007; Jongejans et al. 2008). Nonetheless, to date, few studies have incorporated detailed parameters for all three factors (Jongejans et al. 2008) and we lack understanding of their relative contribution in spatially structured landscapes.

Model accuracy

Our model is one of the first to include detailed parameters for landscape structure, dispersal behaviour and vital rates. We have thereby included all the main processes that govern species' persistence and dispersal through the landscape (Hodgson et al. 2012). We believe our current choice of parameters provides sufficient detail to make meaningful comparisons between groups of species with varying life-histories. Nonetheless, more details could be included in future studies to make the model more realistic. For example, we did not incorporate density dependence of emigration or specific settlement decision rules (see Travis et al. 2012a). Also, our model is restricted to semelparous species (reproduction is limited to a single episode) and to females, without modelling the need for a male for reproduction. In that respect, the species given as examples in the analysis of restoration scenarios are not exact matches to the fixed parameters we used.

We chose our range of parameter values such that it represents realistic values for our study system, but the range of tested values might have been wider for some parameters than for others. This could have affected the exact amount of variance explained by each parameter, but should have limited impact on the order of magnitude of importance of each parameter. In particular the parameter maxspeed had a somewhat unexpected effect. High values of this parameter lead to high extinction rates, as it causes individuals to race through suitable habitat before they have the chance to reproduce. In reality, individuals may move more slowly within small habitat fragments. Therefore, our highest value of maxspeed may be ecologically unrealistic, even though it represents a speed (500 metres per day) that can easily be achieved within suitable habitat by some arthropods. In reality effects of maxspeed may therefore be more limited than suggested by our results.

The only parameter that was purposefully downscaled in our analysis (to increase model speed) is carrying capacity (K). Higher values of K will certainly lead to higher population densities, higher absolute rates of dispersal and smaller chances of extinction. Also, a wider range of tested values for this parameter is likely to make it a more influential parameter for the simulation outcome. This implies that the effect of K on the response variables is likely to be underestimated in our study.

Relative importance of dispersal, vital rates and landscape

Our results demonstrate that all three parameter categories, dispersal traits, landscape structure and vital rates, affect species persistence and spread in fragmented landscapes. A vital rate like age at maturity thus not only alters population densities, but also directly affects expansion rate and whether species spread across the landscape. Population vital rates explained less variation than landscape structure and dispersal traits, but nonetheless were consistently included in the five most influential parameters. Moreover, the effect of population vital rates may even be larger than our results suggest due to potential overestimation of the effects of maximum speed and underestimation of the impact of the carrying capacity (see above). A surprising result is that the dispersal trait perceptual range was consistently unimportant in our analysis. This trait has previously been identified as an important parameter, substantially enhancing connectivity (Pe'er and Kramer-Schadt 2008). Baguette and Van Dyck (2007) argue that any increase in perceptual range should represent a benefit for dispersing individuals in highly fragmented

systems and selection for increased perceptual range in fragmented landscapes has indeed been detected (Merckx and Van Dyck 2007). Our results contradict this. This may in part be due to the very low habitat availability levels in our analysis (1-10%). Pe'er and Kramer-Schadt (2008) demonstrated that the effect of perceptual range was proportional to the percentage of land covered by the structures to which the species responds. In our study the distance between habitat fragments may have been so large that even individuals with a large perceptual range (~1 km) mostly died before reaching suitable alternative habitat. Another factor that may have contributed to our results is that we modelled movement in the matrix to be faster and more directional than movement within habitat patches. This is likely to contribute to more effective arrival in suitable habitat patches independent of perceptual range (Schtickzelle et al. 2007b; Bartoń et al. 2009, 2012).

Interactions

Only a limited proportion (3-5%) of observed variation in our model outcomes was caused by interactions between species traits (dispersal traits and vital rates) and landscape attributes. We did not find any evidence for opposing trait values leading to higher population densities under different landscape settings. We did, however, find that species traits had little influence on functional connectivity at 1% habitat availability, which represents the current availability of calcareous grassland in our study area (Willems 2001). This indicates that even for species with good dispersal ability, functional connectivity is virtually non-existent in the current landscape, warranting great concern for the vulnerability of these communities in particular with regards to predicted climate change. These findings corresponds well with the vast body of literature reporting extinction thresholds due to lack of functional connectivity at low habitat availabilities (Andrén 1994; With and Crist 1995; Bascompte and Sole 1996; Keymer et al. 2000; Travis 2003). Even for good dispersers, extinction thresholds are generally believed to occur around or above 10% habitat availability (Andrén 1994; Travis 2003).

Restoration strategies

Although our alternative restoration scenarios represent rather extreme cases compared to real life, they nevertheless give a good insight in the relative effectiveness of alternative approaches. This analysis also sheds light on the question whether species with different traits require different restoration strategies. We found that responses with respect to total population density were similar across the four selected species groups, indicating that there is little conflict of interest when it comes to the most effective restoration strategy (see also Pe'er et al. 2011; Hodgson et al. 2012). Also with respect to the maximum distance reached after ten years, there were few differences in the ranking order of restoration scenarios between the four species groups. A ten-fold increase in available habitat had the greatest effect for all four species groups both on population density and on maximum distance travelled. Clustered new habitat was equally or more effective than highly fragmented additional habitat patches for boosting population densities. For one species group (FI) a fragmented landscape, however, led to greater travel distances than a clustered landscape. A tenfold increase in available habitat with low habitat contagion had on average a greater effect on population density than a five-fold increase accompanied by greater habitat clustering. However, final population densities in the clustered approach

showed much greater variation, especially for the two non-flying species groups. This indicates that this strategy can be effective, depending on where the clusters are located. Obviously, additional habitat is only of use to species if it is located near enough to existing populations to be reached within a reasonable time frame. Evaluating the effect of restoration strategies on the maximum distance travelled through the landscape within 10 years revealed that the species groups incapable of flight did not travel more than 1.2 km. Thus, all additional habitat created outside this range did not have an effect on their population density. Increasing matrix quality had no effect on population densities and only increased the maximum distance reached for one species group (FL). Increasing matrix quality has often been suggested as an effective restoration measure in the light of climate change, but lacks empirical testing (Heller and Zavaleta 2009). Following our results from the full analysis its effect on dispersal speed may increase with increasing habitat availability. However, considering the very limited overall effect of dispersal mortality on final population density (0.8% explained variance) in our study, the effect of increased matrix quality on species persistence may be low, even at higher habitat availability. This is in agreement with literature reviews performed by Prevedello and Vieira (2010) and Hodgson et al. (2011a), who both found little support for the claim that matrix quality greatly affects species persistence in fragmented landscapes.

Overall, our results show little conflict between species groups when it comes to the most effective restoration strategies. In addition, our results show that landscape structures promoting dispersal speed are not necessarily the same as those promoting species persistence (Hodgson et al. 2011b, 2012). However, conflict only arose for species group FL, which is the group that reached highest dispersal distances in all restoration scenarios and thus depends least on habitat restoration for successful dispersal and range expansion.

Application

As expected, our results demonstrate that all three parameter categories, dispersal traits, landscape structure and vital rates, affect species persistence and spread in fragmented landscapes. This highlights the need to incorporate species specific information related to both dispersal ability and demographic vital rates when studying functional connectivity (Jongejans et al. 2008), especially in relation to climate change (Travis et al. 2013).

With respect to potential restoration scenarios our research indicates that the absolute effect of restoration measures differs markedly between species groups, but the ranking order of restoration scenarios in terms of functional connectivity and species persistence is similar across species, which is in concordance with earlier studies (Pe'er et al. 2011; Hodgson et al. 2012). Interestingly we found that there is also little conflict of interest between scenarios promoting dispersal and species persistence, even though potential for such conflict has repeatedly been reported (Hodgson et al. 2011b, 2012). This discrepancy is in part caused by the very low habitat availability in our study system, causing an increase in habitat availability to be essential for both persistence and functional connectivity. In addition, it seems that the largest discrepancy between scenarios promoting dispersal and scenarios promoting population densities arise in species with good dispersal ability, which are able to disperse best in any given landscape and thus depend least on restoration efforts to survive under climate change. More empirical research is needed to establish

whether this is a general pattern or a specific consequence of our model, but it may limit the applied value of the heated debate on the value of connectivity conservation (Hodgson et al. 2009, 2011a; Doerr et al. 2011). Even under climate change the best restoration strategy seems to be to increase habitat availability nearby existing populations. This lack of conflict is encouraging news for biodiversity conservation. However, our results also give reason for great concern. Even a ten-fold increase in habitat availability only led to an additional range expansion of 200 to 400 metres over 10 years for our non-flying species. With average range shifts of 6.1 km per decade (Parmesan and Yohe 2003), even drastic habitat availability increases may be insufficient to keep up. This suggests that it may be more effective to create heterogeneous habitats with a range of microclimatic conditions within single sites than to rely on range shifts to keep up with macroclimatic conditions.

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Appendix 1. Explained variance

Table A1. Explained variance for each parameter, grouped per category (dispersal traits, landscape attributes, population vital rates and interactions across categories). Results are given for four response variables: 1) extinction of the population, 2) dispersal across the landscape within 10 years, 3) the duration to first arrival at the opposite side of the landscape and 4) the total density in the landscape after 10 years.

Category	Parameter	Dispersal (%)	Extinction (%)	Density (%)	Arrival time (%)
Dispersal	maxspeed	7.2 (2.3)	67.2 (8.7)	5.5 (9.6)	4.3 (20.8)
	maxspeed*percange	0 (0)	0 (0)	0 (0)	0 (0)
	Mudisp	12.8 (3.1)	2.9 (1.8)	0.8 (3.5)	25 (49.9)
	Mudisp*maxspeed	0.1 (0.3)	0.4 (0.7)	0 (0)	0 (1.8)
	Mudisp*percange	0 (0)	0 (0)	0 (0)	0 (0)
	Mudisp*speedfact	0 (0)	0 (0.2)	0 (0)	0.1 (3.2)
	pcross	1.6 (1.1)	7 (2.8)	16.3 (16.4)	0 (0)
	pcross*maxspeed	0.7 (0.7)	0.7 (0.9)	14.6 (15.6)	0.1 (3.4)
	pcross*Mudisp	0 (0.1)	0 (0)	0 (0.4)	0 (2)
	pcross*percange	0 (0)	0 (0)	0 (0)	0 (0)
	pcross*speedfact	0 (0)	0 (0.2)	0 (0)	0 (0)
	percange	0 (0)	0 (0)	0 (0)	0 (0)
	speedfact	0.2 (0.4)	0.1 (0.4)	0 (0.8)	0.1 (2.9)
	speedfact*maxspeed	39.2 (5.4)	0.2 (0.5)	1.5 (5)	43.2 (65.6)
	speedfact*percange	0 (0)	0 (0)	0 (0)	0 (0)
Landscape	H	0.1 (0.3)	0.3 (0.6)	0.6 (3)	1 (9.9)
	P	26.6 (4.5)	10.3 (3.4)	37.1 (24.8)	8.4 (28.9)
	P*H	1.4 (1)	0 (0.1)	0.1 (1.2)	0.1 (3.6)
Vital rates	AAM	5.6 (2)	4.3 (2.2)	10.4 (13.1)	7.2 (26.9)
	AAM*K	0 (0)	0.1 (0.3)	0 (0)	0 (1.9)
	K	0.5 (0.6)	1.1 (1.1)	7.1 (10.8)	0.8 (9)
Interaction	AAM*H	0.2 (0.4)	0 (0)	0 (0)	0 (0)
	AAM*maxspeed	0.1 (0.2)	0.8 (0.9)	0.3 (2.3)	0 (0.4)
	AAM*Mudisp	0.3 (0.5)	0 (0.2)	0.1 (1)	0.2 (4.7)
	AAM*P	0.3 (0.4)	0.2 (0.4)	1.1 (4.2)	0.2 (4.6)
	AAM*pcross	0.1 (0.3)	0.2 (0.5)	0.3 (2.2)	0 (0.7)
	AAM*percange	0 (0)	0 (0)	0 (0)	0 (0)
	AAM*speedfact	0 (0)	0 (0.2)	0 (0.1)	0 (0)
	K*H	0 (0.1)	0 (0)	0 (0)	0 (2)
	K*maxspeed	0 (0)	0.2 (0.5)	0 (0)	0 (1.9)
	K*Mudisp	0 (0)	0 (0)	0 (0)	0 (0)
	K*P	0 (0)	0 (0.1)	0 (0)	0 (1)
	K*pcross	0 (0.1)	0 (0)	0 (0)	0 (0)
	K*percange	0 (0)	0 (0)	0 (0)	0 (0)
	K*speedfact	0 (0)	0 (0)	0 (0)	0 (0)
	maxspeed*H	0.1 (0.3)	0.1 (0.3)	0 (0.5)	0.1 (3)
	maxspeed*P	0.5 (0.6)	1 (1.1)	1 (4.1)	1.1 (10.4)
	Mudisp*H	0.4 (0.6)	0.1 (0.3)	0.1 (1.2)	0.1 (3.1)
	Mudisp*P	0.1 (0.3)	1.2 (1.2)	0.2 (1.9)	0.5 (7.2)
	pcross*H	0.1 (0.3)	0 (0)	0.4 (2.7)	0 (2.1)
	pcross*P	1 (0.9)	0.3 (0.6)	1.5 (4.9)	0.7 (8.2)
	percange*H	0 (0)	0 (0)	0 (0)	0 (0)
	percange*P	0 (0)	0 (0)	0 (0)	0 (0)
	speedfact*H	0 (0)	0 (0.1)	0 (0.1)	0 (0.9)
	speedfact*P	0 (0)	0.1 (0.4)	0 (0)	0 (0)
Residual		0.7 (0)	1.1 (0)	1 (4.1)	6.4 (25.3)

The Bombardier beetle (*Brachinus crepitans*) (Photo: Theodoor Heijerman)



Chapter 7

Species-area relationships are modulated by trophic rank, habitat affinity and dispersal ability

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Abstract

In the face of ongoing habitat fragmentation, species-area relationships (SARs) have gained renewed interest and are increasingly used to set conservation priorities. An important question is how large habitat areas need to be to optimize biodiversity conservation. The “area-per se hypothesis” states that SARs are governed by colonization-extinction dynamics. Small sites harbour small populations, which are more prone to extinction than the large populations sustained by large sites. In addition, colonization-extinction dynamics are predicted to depend on trophic rank, habitat affinity and dispersal ability of the species. Empirical evidence for the effect of these species characteristics on SARs remained inconclusive.

In this study we used a large dataset of carabid beetles in calcareous grasslands to investigate how calcareous grassland area affects species richness and activity density for species differing in trophic rank, habitat affinity and dispersal ability. In addition, we investigated how SARs are affected by the availability of additional calcareous grassland in the surrounding landscape.

Our results demonstrate that carabid beetle species richness and activity density increase with calcareous grassland area for zoophagous typical dry grassland species and to a lesser extent for zoophagous habitat generalists. Phytophagous species and zoophagous forest and wet grassland specialists were not affected by calcareous grassland area. The dependence of species on large single sites increased with decreasing dispersal ability for species already vulnerable to calcareous grassland area. Additional calcareous grassland in the landscape had a positive effect on local species richness but this effect was restricted to a few hundred meters.

Our results demonstrate that SARs are affected by trophic rank, habitat affinity and dispersal ability. These species characteristics do not operate independently but should be viewed in concert. In addition, the landscape context modulates the effect of specific trait attributes. Our data suggest that the impact of habitat area on trophic interactions may be larger than previously anticipated. In small habitat fragments surrounded by a hostile matrix, food chains may be strongly disrupted. This highlights the need to conserve continuous calcareous grassland patches of at least several hectares in size.

Keywords

Biodiversity, body size, community, flight ability, food chain, fragmentation, generalist, SAR, specialist, trait, trophic level, nature conservation

Introduction

Species-area relationship (SAR) theory predicts that species richness increases with area (Williams 1943; Preston 1960; MacArthur and Wilson 1967). There are two main ecological mechanisms underlying this long-standing and rigorously tested ecological theory, which are not mutually exclusive. First, large areas tend to contain a larger diversity of environmental conditions and biotopes, which support a greater variety of species (Williams 1964), because species differ in resource requirements and environmental tolerance to abiotic conditions. This is called the “habitat-diversity hypothesis”. The second mechanism, termed the “area-per se hypothesis” is derived from the extinction-colonization equilibrium underlying classical island biogeography theory (MacArthur and Wilson 1967). Extinction rates increase with decreasing population size (Hanski 1999; Henle et al. 2004) and population density generally increases or remains constant with increasing area (Connor et al. 2000). This implies that small sites harbour small populations, which are more prone to extinction than the large populations sustained by large sites. SARs have recently received renewed interest in the light of conservation ecology and are increasingly used to predict extinction rates of target species for nature conservation (e.g. Hanski et al. 2013) and to prioritize conservation efforts (e.g. Steffan-Dewenter and Tschardtke 2000). An important question in this respect is how large habitat areas need to be to optimize biodiversity conservation.

The minimum area of habitat required to support a viable community relates to the ‘area-per se hypothesis’, which predicts that SARs depend on species-specific colonization-extinction dynamics. Extinction rates decrease with habitat area (MacArthur and Wilson 1967), while colonization rates are predicted to decrease with habitat isolation (MacArthur and Wilson 1967). This implies that SARs are also affected by the landscape context (Hanski 1999; Hanski et al. 2013). Additional habitat in the landscape will increase metapopulation persistence and hence colonization chances (Hanski 1999). Here it is worth noting that SAR theory was initially developed for real islands, where the surrounding matrix is clearly not suitable habitat for all terrestrial species. When applying these principles to ‘islands’ of a specific biotope (e.g. calcareous grassland) surrounded by other land-use types (e.g. arable land) the relationship becomes more complex (Haila 2002; Shepherd and Brantley 2005). While the matrix may be hostile and unsuitable for specialist species, which perceive their habitat as fragmented, the landscape may provide continuous habitat for generalist species (Driscoll et al. 2013). A species’ habitat affinity is thus likely to alter its response to biotope area and site isolation (De Vries et al. 1996; Davies et al. 2000; Swihart et al. 2003).

In addition to habitat affinity, which governs how species perceive the landscape, there are a number of other factors that affect extinction-colonization dynamics. Colonization rates increase with increasing dispersal ability (Den Boer 1990a; Tschardtke et al. 2002a). Extinction rates are governed by several species characteristics (Verberk et al. 2010b), including body size (Damuth 1981; Blackburn 1993) and trophic rank (Holt et al. 1999). Body size has repeatedly been identified as a trait that negatively affects population density, but the cause of this pattern has been questioned, as body size is correlated to several other traits affecting population density, including trophic rank (Tschardtke et al. 2002a; Henle et al. 2004). Trophic rank affects extinction rates

because species from higher trophic ranks (carnivores and parasites) generally have both lower population densities (Henle et al. 2004; Verberk et al. 2010b) and increased population fluctuations (Holt et al. 1999; Tschardtke and Kruess 1999; Henle et al. 2004; Van Nouhuys 2005). The rationale behind this is that less energy is transferred through each successive link in the food chain, causing predators to be less abundant than prey of comparable body size and reproductive rate due to energetic limitations (Hutchinson 1959; Heino 2008). In addition, populations of higher trophic rank are likely to exhibit stronger numerical fluctuations, as fluctuations of food (or prey or host) sources are exacerbated as they cascade up the food chain (Holt et al. 1999; Van Nouhuys 2005). In spite of this theoretical underpinning, empirical evidence for the effect of trophic rank on the SAR has been inconsistent (Van Nouhuys 2005) and it has been suggested that increasing SAR slopes with increasing trophic rank should be limited to food specialists (Steffan-Dewenter and Tschardtke 2002; Henle et al. 2004). A complicating factor is that most studies to date have been carried out in plant-herbivore and host-parasite systems (Tschardtke et al. 2002b; Van Nouhuys 2005), where the species belonging to different trophic levels differ in many more respects. In these cases the general differences in body size and dispersal ability between the investigated trophic ranks, may alternatively explain the observed patterns, rather than trophic rank per se.

In this study we aim to investigate first, how the area of a single biotope type affects species richness for a range of species that belong to a single monophyletic taxon but differ in trophic rank, dispersal ability and habitat affinity. Secondly, we investigate how SARs for this group of species are affected by habitat isolation. We use carabid beetles as a focal group because they exhibit considerable variation in trophic rank, dispersal ability and habitat affinity (Turin 2000). This provides a unique opportunity to study the effect of trophic rank on SAR independent of major body-plan constraints. We performed this study in calcareous grasslands because this habitat is of high conservation value (WallisDeVries et al. 2002) and has become highly fragmented over the past century across Europe (Baldock et al. 1996; WallisDeVries et al. 2002). Using a meta-analysis of datasets from Northwestern Europe we test the hypothesis that carabid beetle species richness will increase with calcareous grassland area. As we expect that such increases are caused by an increase in population viability (following the area-per se hypothesis), we expect carabid beetle activity density to increase likewise. We hypothesize that the minimum area required for viable communities increases throughout the trophic chain due to the above mentioned shifts in population density and stability. This should cause zoophagous species to respond more strongly to calcareous grassland area than phytophagous species. We also predict that flightless species will be restricted to larger sites than species possessing good flight ability and that additional calcareous grassland in the surrounding landscape will positively affect carabid beetle richness in accordance with metapopulation theory (Hanski 1999). Given the differences between species in their perception of the landscape we hypothesize that all of these patterns will be contingent upon the habitat affinity of a species. The above predictions should only hold for carabid beetles that are restricted to calcareous grassland, while habitat generalists and typical species of wet grassland and forests found in calcareous grasslands will not be affected by the area of calcareous grassland sites.

Methods

Study system

Calcareous grasslands in Northwestern Europe have a distinct carabid beetle fauna, consisting mainly of thermophilic species, which are restricted to nutrient-poor grasslands with a warm microclimate (Lindroth 1949). In addition, calcareous grasslands are inhabited by a group of eurytopic species, which occur in various arable and grassland habitats (Turin 2000). The total area of unimproved calcareous grassland has declined sharply over the past century (Baldock et al. 1996; WallisDeVries et al. 2002). Remaining sites are mostly surrounded by arable land, fertilized grasslands and woodland.

Carabid beetle data collection

We collected six datasets from four countries in Northwestern Europe containing pitfall trap data of carabid beetles from unimproved calcareous grasslands (see Appendix 1). Descriptions of the sampling regions and vegetation types of these datasets are given in Willems (2001), Regan and Brown (in prep), Dufrêne (1990), Eckel (1988) and Hannig et al. (2005). The exact trapping method differed between datasets, but was consistent within each dataset (Table 1). For the analyses, all data were pooled per calcareous grassland site.

Table 1. Specifications of the datasets included in the analysis. 'Symbol' refers to the symbols used in the figures.

Nr	Country	Nr of sites	Traps per site	Trap ø	Season	Trapping days	Year	Method reference	Symbol
1	Germany	3	20	8.5 cm	Apr.-Oct.	200	2006	Van Noordwijk et al. 2012, chapter 3	●
2	Netherlands	15	10	8.5 cm	Apr.-Oct.	200	1988	Van Noordwijk et al. 2012, chapter 3	▲
3	Germany	4	10	8.5 cm	March-Oct.	220	1986 or 1987	Eckel 1988	+
4	Germany	4	15-20	9 cm	All year	730	1995 and 1996	Hannig et al. 2005	□
5	Ireland	19	10	7 & 9 cm	May-August	55	2006	E. Regan pers. com.	■
6	Belgium	13	10	8.5 cm	Apr.-Oct.	185	1986 or 1987	Dufrêne 1990	✱

Species characteristics

For each species in our dataset we determined trophic rank, habitat affinity, dispersal ability and mean body size from literature (see Appendix 2). Habitat affinity was categorized following Turin (2000) and Desender et al. (2008) with “dry grassland specialists” defined as all species mainly occurring in dry, nutrient poor habitats including calcareous grasslands and heathlands, “wet/forest specialists” defined as species mainly occurring in wet habitats and forests and “open habitat generalists” defined as all species occurring in a wide range of open habitats, including agricultural land. We distinguished three trophic groups based on Turin (2000) and Saska (2004, 2005): 1) species that are phytophagous throughout their life cycle (referred to as phytophagous), 2) species that are at least partly zoophagous throughout their life-cycle, thus including zoophytophagous species (referred to as zoophagous) and 3) species which are phytophagous as adults, but zoophagous as larvae (referred to as trophic level shift). The species which shift in trophic rank during their life-cycle were defined as a separate group, because we suspect that larvae are the most critical stage (Thiele 1977), which would cause these species to behave like zoophagous species. To date however, these species have generally been classified as phytophagous species, because most studies only incorporate adult feeding habits (see e.g. Ribera et al. (1999) and Vanbergen et al. (2010)). Dispersal ability was classified based on a combination of wing morphology, flight muscle development and flight records from window traps, following Den Boer (1990b), Turin (2000) and Desender et al. (2008). We distinguished three categories: poor dispersers (species incapable of active flight), intermediate dispersers (species capable of flight but with few flight records or low proportions of macropterous individuals) and good dispersers (species with a large proportion of the population capable of active flight and regularly caught in window traps). The final species characteristic included in our analysis was body size, measured as the total body length in mm, which was derived from Desender et al. (2008).

GIS analysis

We mapped each calcareous grassland site on aerial images in ArcGis 9.2 (ESRI Inc., Redlands, CA, USA). Where available we used high quality free web mapping services (e.g. Bing maps and Google maps). For some of the Irish sites the quality of freely available aerial photographs was insufficient, instead we used 1m resolution orthophotography maps supplied by Ordnance Survey Ireland. On all maps, good quality (i.e. nutrient poor, well managed) calcareous grassland could quite easily be distinguished from other habitat types, including more nutrient-rich or abandoned grassland, due to clear colour differences. Site boundaries were always checked by people with field knowledge of the sites. In addition to the sampled sites, we mapped all good quality calcareous grassland sites in a 1000m radius around the centre point of each sampling site. For each site we calculated the area of calcareous grassland (m²) within each sampling site and the area of calcareous grassland within a 500m and 1000m radius of the sampling site (excluding the sampling site itself). These spatial scales were chosen based on the fact that flightless individuals generally do not cover distances of more than a few hundred metres in their lifetime (Den Boer 1970; Thiele 1977).

Statistical analysis

Generalized linear mixed models were used to analyse the data, with dataset as a random variable to account for regional differences in carabid beetle assemblage and differences in sampling intensity between datasets. All analyses were performed separately for the three habitat affinity groups, typical dry grassland specialists, generalist open habitat species and wet grassland and forest specialists (see above). It turned out that the Irish dataset contained only three species classified as typical dry grassland species, one for each trophic level (seven individuals in total). Even when adapting habitat affinity criteria to Irish standards only few species could be characterised as being typical for dry grasslands (Anderson et al. 2000). This is most likely due to the wetter and cooler climate in Ireland in combination with its impoverished island fauna (Good 2004). For this reason the Irish dataset was excluded from the analysis for typical dry grassland specialists. For the analyses of generalist and wet grassland and forest species, the Irish dataset did not differ structurally from the mainland datasets and was hence included, after checking that the difference in the number of included datasets between habitat affinity groups did not affect the results. Models were constructed for two response variables, species richness and activity density. Activity density data were natural log transformed to reduce the effect of highly active species (Ribera et al. 2001; Vanbergen et al. 2010). Both species richness and activity density (natural log transformed) followed a Poisson distribution. All habitat size parameters were natural log transformed, in accordance with general species-area relationship theory (Connor and McCoy 1979). For both response variables seven models were constructed (intercept only, calcareous grassland size and calcareous grassland size * trophic rank, the latter two with no additional landscape parameter, with additional calcareous grassland at the 500m scale or with additional calcareous grassland at the 1000m scale), using the lmer function in R (R Core Development Team 2013) package lme4 (Bates et al. 2013). Models were fit using the Laplace approximation and optimizing the log-likelihood rather than the REML criterion, as this method is better suited when comparing models with varying fixed effects. Because the random part of the seven models was identical, AIC scores were used to rank models. Model averaging over all models scoring within 15 AIC points of the best model was used to obtain parameter estimates and significance values (Bolker et al. 2009).

The effect of dispersal ability on SARs could only be tested in a meaningful way within trophic ranks and habitat affinity groups, due to trait correlations (species with poor dispersal power were all zoophagous). However, due to such data partitioning, the number of species per dispersal group was rather low (as low as three species per group). Therefore, we did not test for differences in species richness with increasing calcareous grassland size between dispersal ability groups. Instead, we tested whether the range of calcareous grassland sizes in which species were found, differed between dispersal ability groups, providing an indication of the area requirements of each group. To do this, we used Levene's test (centred around the median rather than the mean of each group, to account for slight deviations from a normal distribution), as we were interested in the range of site sizes, rather than the mean size of sites in which species of each group occurred.

Results

Species-area relationships

The six datasets combined held a total of 23,540 carabid beetles belonging to 141 species. Of these, 2,983 individuals (13%) and 48 species (34%) were classified as dry grassland specialists. Both species richness and activity density for all three habitat affinity groups were best explained by models including calcareous grassland size, trophic level and a measure of additional calcareous grassland in the landscape (Appendix 3). Additional calcareous grassland in the landscape significantly increased the local species richness for both typical dry grassland species and open habitat generalists, but not for forest and wet grassland species (Table 2). This effect was most pronounced when only including additional calcareous grassland within a 500m radius and was only marginally significant when including all additional calcareous grassland within a 1000m radius. Activity density

Table 2. Model averages for the fixed effects parameters in the best three generalized linear mixed models for species richness per habitat affinity group. Significant effects are marked: * $p < 0.05$, ** $p < 0.01$.

Fixed effect	Estimate	Std. Error	z value	p
<i>Dry grassland</i>				
(Intercept)	-4.47185	1.27327	-3.510	0.001**
Area	0.48402	0.11654	4.153	<0.001**
Trophic level shift	-0.47318	3.38273	-0.140	0.889
Phytophagous	4.46496	1.40646	3.174	0.002**
Area * Trophic level shift	-0.16320	0.31918	-0.512	0.608
Area * Phytophagous	-0.39842	0.13283	-2.999	0.003**
Additional calc. grass. 500m	0.04914	0.01597	3.076	0.002**
Additional calc. grass. 1000m	0.03574	0.01578	2.265	0.023*
<i>Generalist</i>				
(Intercept)	0.75861	0.437154	1.747	0.120
Area	0.07929	0.038182	2.075	0.046*
Trophic level shift	-1.41957	1.068687	-1.328	0.184
Phytophagous	0.26232	0.643510	0.4073	0.684
Area * Trophic level shift	-0.06933	0.100987	-0.686	0.492
Area * Phytophagous	-0.11146	0.061102	-1.824	0.068
Additional calc. grass. 500m	0.03654	0.009807	3.726	<0.001**
Additional calc. grass. 1000m	0.02017	0.009572	2.107	0.035*
<i>Forest & wet grassland</i>				
(Intercept)	1.43105	0.403642	3.555	0.001**
Area	0.04255	0.035250	1.206	0.235
Trophic level shift	-2.87945	1.467678	-1.962	0.050*
Phytophagous	-0.63522	0.837104	-0.759	0.448
Area * Trophic level shift	-0.01780	0.137981	-0.129	0.897
Area * Phytophagous	-0.11725	0.080532	-1.456	0.145
Additional calc. grass. 500m	0.01727	0.009739	1.774	0.076
Additional calc. grass. 1000m	0.01738	0.009585	1.813	0.070

of typical dry grassland carabids was not affected by additional calcareous grassland nearby (Appendix 4). However, activity density of open habitat generalists increased with additional calcareous grassland, especially at the 500m scale.

Trophic rank

Trophic rank significantly affected species-area relationships, but only for typical dry grassland carabid species (nearly so for generalist species) (Figure 1, Table 2). Within the typical dry grassland species, phytophagous species were less affected by calcareous grassland size than zoophagous species (significant interaction: area * phytophagous). The SAR for species which shift in trophic rank during their life-cycle did not differ from purely zoophagous species (Figure 1, Table 2). It should be noted however, that

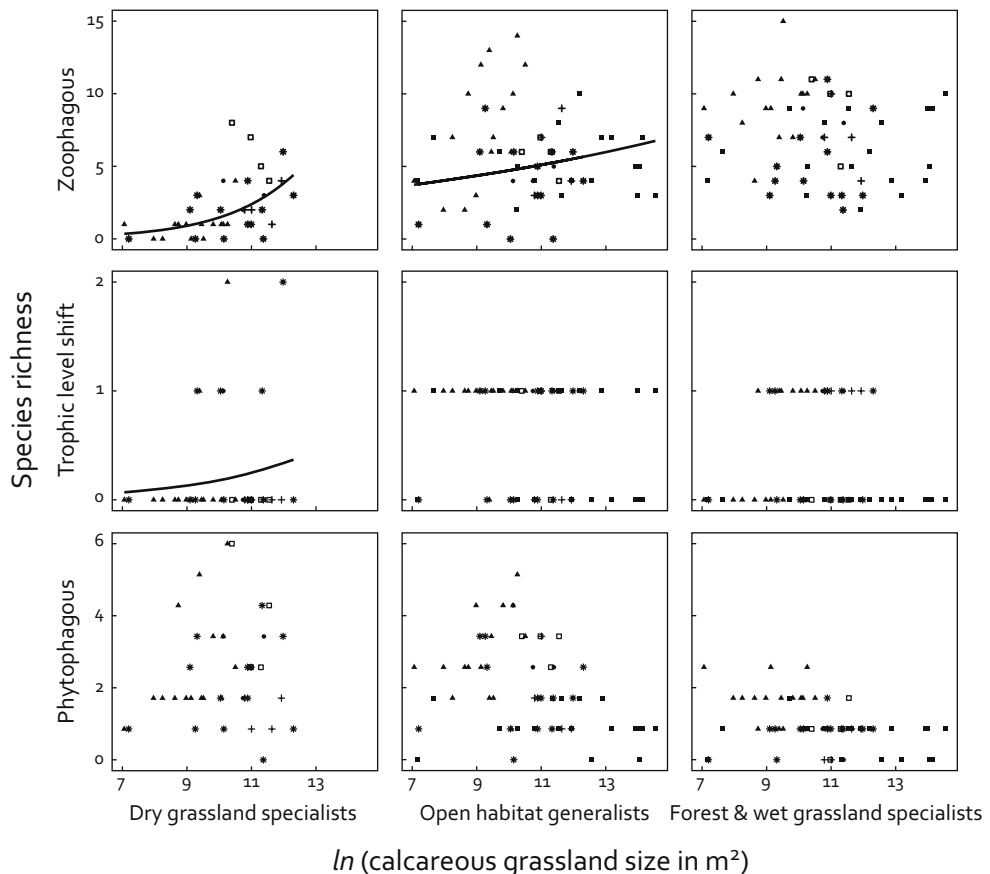


Figure 1. Species richness of zoophagous species (upper panels), phytophagous species with zoophagous larvae (middle panels) and phytophagous species (lower panels) as a function of calcareous grassland size (natural log scale). Species are grouped by habitat affinity: typical dry grassland species (left), generalist open habitat species (middle) and wet grassland and forest species (right). Symbols represent different datasets (see Table 1). Fitted lines (Poisson GLMM) are plotted where significant effects of calcareous grassland size on species richness were found (see Table 2).

the number of species shifting in trophic rank was limited (six species in total). Activity density was affected by trophic rank in much the same way as species-richness (see Appendix 4).

Dispersal ability

The range of occupied grassland sizes differed significantly between dispersal groups for zoophagous dry grassland carabid beetles (Levene's test; $F_{2,54} = 4.53$, $p = 0.015$), but not for other trophic groups or for habitat generalists (Levene's test; $F < 0.50$, $p > 0.50$). Species with poor dispersal ability were only found in the largest sites, while species with good dispersal ability were found in the widest range of sites (Figure 2). These patterns were the same across body-sizes (see Appendix 5).

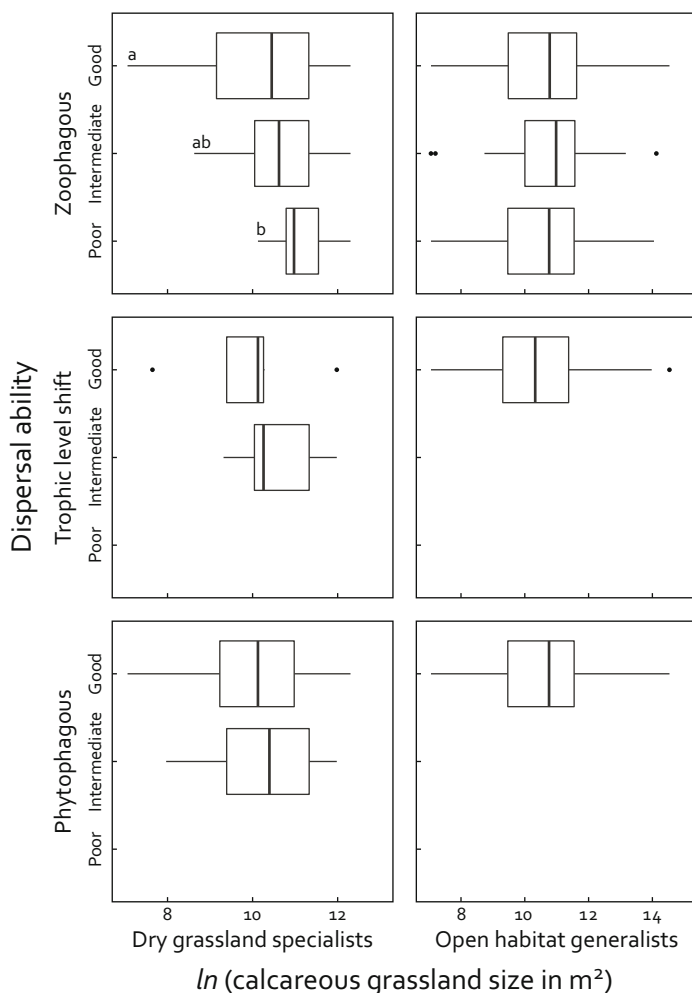


Figure 2. Boxplots of occurrences of typical dry grassland (left) and generalist open habitat (right) carabid beetles in calcareous grasslands of varying sizes by flight ability. Different letters indicate significantly different ($p < 0.05$) variances of calcareous grassland size between flight ability groups.

Discussion

Our meta-analysis demonstrates that carabid beetle species richness and activity density increase with calcareous grassland size, depending on both habitat affinity and trophic rank of the species. This is one of the first studies reporting such an effect of trophic rank within a single monophyletic group that mainly consists of food generalists. We also demonstrate that additional calcareous grassland in the surrounding landscape has a positive effect on local species richness and that the dependence of species on large single sites increases with decreasing dispersal ability for carnivorous habitat specialists.

Species-area relationships

It has repeatedly been shown that SAR theory, which was initially developed for real islands, also applies to 'islands' of a specific biotope (e.g. calcareous grassland) surrounded by other land-use types (Davies et al. 2000; Steffan-Dewenter and Tscharnkte 2000; Hanski et al. 2013). However, in contrast to real islands, the matrix surrounding biotope islands may be perceived as habitat by some (generalist) species, making SARs more spurious (Davies et al. 2000; Shepherd and Brantley 2005; Driscoll et al. 2013). In concordance with this, we demonstrated that carabid species richness only strongly increased with calcareous grassland size for typical dry grassland species. This demonstrates the importance to adopt an organism-centered understanding of landscapes and habitat patches (Shepherd and Brantley 2005). Incorporating species' habitat affinity proved to be a valuable tool to better understand relationships between area and species richness (see also De Vries et al. 1996), although it remains difficult to divide species over habitat affinity classes. Habitat affinity cannot be measured independent of a species' environment (see Violle et al. 2007). It is generally inferred from distribution records and therefore depends on the landscape context and the availability of records. This means that the habitat affinity of a species may be perceived to be more limited than it really is, just because the species has never been recorded from specific biotopes in which it can occur. Alternatively, species may seem to have a wider tolerance of habitat conditions than they actually have, because they can occur both in semi-natural grassland and on arable land, but only under specific circumstances. This seems to be the case for at least some of the generalist species in our study, as generalist zoophagous carabid beetle richness increased with calcareous grassland area. Apparently some of the species classified as generalists and assumed to be well capable of surviving in the mainly arable matrix, were still more or less restricted to calcareous grassland, at least in some landscape settings. With increasing sampling intensity, habitat affinity classification becomes more accurate, but its predictive power remains low as long as the causal mechanism underlying this affinity remains unknown.

Landscape context and dispersal ability

Additional calcareous grassland in the vicinity had a positive effect on species richness for typical dry grassland carabid beetles in our study, as would be expected from island biogeography theory (MacArthur and Wilson 1967). Surprisingly, this effect was also found for habitat generalists, indicating again, that the surrounding matrix landscape does not form suitable habitat for all of these species. The spatial extent of the effect of

additional calcareous grassland was limited to a few hundred meters, demonstrated by the stronger effect of additional calcareous grassland at the 500m compared to the 1000m scale. In addition, the positive effect of additional calcareous grassland in the landscape proved to be much weaker than the effect of increased area. Additional calcareous grassland in the landscape only affected species richness but not activity-density of typical dry grassland species. This indicates that the influx of individuals from these additional areas is too small to affect local population densities, but high enough to offer increased recolonization chances after local extinction, contributing to community resilience.

Dispersal ability affects species' vulnerability to habitat isolation (Den Boer 1990a; Wamser et al. 2012). We demonstrated that this also leads to a restriction of poor dispersers to larger sites, at least for zoophagous, dry grassland species. This is in concordance with previous studies by De Vries et al. (1996). Although dispersal ability is correlated to body-size in carabid beetles (all large species are flightless), we could demonstrate that the effect found here is most likely caused by flight ability itself.

Trophic rank modulates SAR

Our results clearly demonstrate that zoophagous carabid beetles respond more strongly to calcareous grassland area than phytophagous species. Our results also indicate that phytophagous species with zoophagous larvae respond similar to completely zoophagous species, rather than to phytophagous species, to which group they are usually assigned (e.g. Ribera et al. 1999; Vanbergen et al. 2010). However, the number of species shifting in trophic rank during their life-cycle is limited (six species in our dataset), so these results should be interpreted with caution.

An effect of trophic rank on SAR was previously predicted (Holt et al. 1999) and empirically demonstrated (Steffan-Dewenter and Tscharncke 2000; Van Nouhuys 2005). However, these studies argued that the slope of SARs should only increase with trophic rank for food specialists (e.g. parasitoids or monophagous consumers) as generalists can compensate for low availabilities of one food source by feeding more on an alternative source, hence showing less population fluctuation. Additionally, food generalists, being able to process multiple food sources, are predicted to have higher population densities (Brown 1984). In contrast, our results suggest that trophic rank *per se*, i.e. irrespective of food specialization, affects the slope of SARs. The zoophagous carabid beetles for which we have found an increased dependence on calcareous grassland area, generally feed on a wide array of prey species (Thiele 1977; Turin 2000) and are thus food generalists. A wide range of food sources may be insufficient to buffer against adverse conditions when all food sources fluctuate in a synchronized manner, e.g. as a response to drought or other adverse weather conditions. Moreover, population densities, which affect extinction rates, were previously found to be lower for zoophagous species than for phytophagous species across a wide array of species with differing food specialization (Verberk et al. 2010b). Several previous studies (Holt et al. 1999; Steffan-Dewenter and Tscharncke 2000, 2002; Van Nouhuys 2005) did not find strong SARs for higher trophic rank generalists, in contrast to our results. In both parasitoids and butterflies, the two main groups previously used to study effects of trophic rank on SAR, food specialism is however, strongly correlated to habitat specialisation and often also dispersal power (Bink 1992; Van Nouhuys 2005).

Thus, the differences found between food generalists and specialists may represent a different perception of the landscape (more continuous versus highly fragmented) rather than a different area dependence arising from food specialisation.

This implies that the impact of habitat size on trophic interactions may be larger than previously anticipated, affecting both food specialists and generalists at higher trophic levels. This conclusion resonates well with studies on the effects of forest fragmentation, which have demonstrated that carnivores respond more strongly to forest fragmentation than lower trophic ranks, independent of food specialisation (Didham et al. 1998; Davies et al. 2000). The distinction between food specialisation and habitat specialisation may seem trivial, especially as they are frequently interrelated, but several authors have previously argued that keeping them separate is important to better understand large scale patterns (Gaston et al. 1997; Verberk et al. 2010b). Our results also suggest vital repercussions for the importance of the landscape context. If only food specialists depend on larger sites, the number of generalist predators in a small site would be independent of the matrix quality. However, if the area dependence of species is governed by habitat affinity, species richness and density of predators in small sites declines sharply with decreasing matrix quality. This creates potential for strongly disrupted food chains in habitat fragments surrounded by a hostile matrix, which could, for example, lead to spill-over effects of phytophagous pest species into agricultural land (Kruess and Tscharntke 1994; Tscharntke et al. 2005). This adds to recent concerns that habitat loss may lead to serious community instability and potentially threatens ecosystem service provision (Spiesman and Inouye 2013).

Implications

Our results demonstrate that the effect calcareous grassland area has on species richness of carabid beetles, is affected by trophic rank and habitat affinity (affecting local extinction chances) in combination with dispersal ability (affecting recolonization rates). Interestingly, recent reviews found insufficient or inconsistent proof for the importance of all three of these species' characteristics for SAR (Henle et al. 2004; Van Nouhuys 2005). This apparent discrepancy is caused by the fact that species characteristics do not operate independently (Davies et al. 2004; Van Kleef et al. 2006; Verberk et al. 2013). For example, traits related to recolonization rates (dispersal ability) only become important for species exhibiting characteristics which increase their local extinction chances (combination of zoophagous and habitat specialist).

In addition, we found that the landscape context modulates the effect of specific species characteristics. Additional patches of calcareous grassland in the surrounding landscape can supplement the biodiversity of a particular location, but only with species with good dispersal ability and over short distances. Matrix quality will affect to what extent habitat generalists can inhabit the matrix and hence to what extent they are limited by the area of one biotope type. In a hostile matrix, habitat generalists are expected to encounter the same restrictions as habitat specialists, causing them to respond in the same way to site size.

Our results indicate that of all dry grassland specialists, zoophagous species are disproportionally affected by habitat fragmentation. In the six datasets, spanning four North-West European countries, zoophagous species typical of dry grasslands with poor dispersal ability, were virtually absent from calcareous grasslands smaller than 5 ha. Trophic interactions may thus be seriously disrupted in smaller sites, especially if they are surrounded by a hostile matrix. This highlights the need to conserve calcareous grassland patches of at least several hectares in size.

Acknowledgements

We thank all site managers for their kind permission to conduct research on their premises. Many thanks go to Hans Matheve and Karin Bisschop for their invaluable help with the GIS analysis. This research was conducted with financial support from Gent University (BOF, joint PhD grant) and Radboud University Nijmegen.

Appendix 1 Data selection method

We collected six datasets from four countries in Northwestern Europe containing pitfall trap data of carabid beetles from unimproved calcareous grasslands (Figure A1). Some datasets included additional data from improved grasslands or forests, but these were excluded for our analysis. Two sites (Thier de Lanaye and Ahrhütte) occurred in more than one dataset. To prevent pseudo-replication, these were only included once (the most extensively sampled instance was retained). Our goal was to gain an equal sample of the carabid beetle fauna of calcareous grasslands differing in size. Most datasets were collected for this purpose and thus consisted of an equal number of pitfall traps per site. Where this was not the case (i.e. where larger sites were sampled more intensively than small sites), a subsample of available trapping stations was taken to attain equal sampling intensity. This was done by identifying pairs of pitfall trap series very close to each other or in very similar vegetation structures (within the calcareous grassland) and randomly selecting one pitfall trap series from each pair. In this way we simulated the initial selection procedure for sampling locations in small sites (i.e. researchers generally selected sampling stations such that they together covered the main habitat variation within each calcareous grassland site). With respect to temporal sampling intensity, sites within each dataset were generally sampled simultaneously and for the same length of time. In some cases sampling continued for a longer period in a selection of sites. These additional data were excluded to attain an equal sampling duration across sites within each dataset.



Figure A1. Sampling locations in Northwestern Europe. Symbols represent different datasets: ● = 1 Germany (2006); ▲ = 2 Netherlands (1988); + = 3 Germany (1986); □ = 4 Germany (1995); ■ = 5 Ireland (2006); * = 6 Belgium (1986).

Appendix 2

Table A1. Characteristics of the carabid beetle species. Body size is given in mm. Category refers to the habitat affinity category (1 = dry grassland specialist, 2 = open habitat generalist, 3 = wet/forest specialist). Flight ability is categorized as poor (1), intermediate (2) or good (3). Trophic level is categorized as zoophagous (1), trophic level shift, for zoophagous larvae with phytophagous adults (2) and phytophagous (3).

Species	Body size	Category	Flight ability	Trophic level
<i>Abax ovalis</i>	14	3	1	1
<i>Abax parallelepipedus</i>	18	3	1	1
<i>Abax parallelus</i>	16	3	1	1
<i>Agonum emarginatum</i>	8	3	3	1
<i>Agonum fuliginosum</i>	7	3	1	1
<i>Agonum muelleri</i>	8	2	3	1
<i>Amara aenea</i>	7	2	3	2
<i>Amara aulica</i>	13	3	3	3
<i>Amara bifrons</i>	6	1	3	3
<i>Amara communis</i>	7	3	3	2
<i>Amara consularis</i>	9	1	3	2
<i>Amara convexior</i>	7	1	3	3
<i>Amara cursitans</i>	8	1	3	3
<i>Amara curta</i>	7	1	2	2
<i>Amara equestris</i>	9	1	3	3
<i>Amara eurynota</i>	10	1	3	3
<i>Amara familiaris</i>	6	2	3	3
<i>Amara lucida</i>	5	1	3	3
<i>Amara lunicollis</i>	8	3	3	3
<i>Amara montivaga</i>	8	1	2	3
<i>Amara nitida</i>	7	1	2	3
<i>Amara ovata</i>	9	1	3	2
<i>Amara plebeja</i>	6	3	3	3
<i>Amara praetermissa</i>	7	1	3	2
<i>Amara pulpani</i>	7	1	2	3
<i>Amara similata</i>	9	2	3	3
<i>Amara tibialis</i>	4	1	3	3
<i>Anchomenus dorsalis</i>	7	2	3	1
<i>Anisodactylus binotatus</i>	10	3	3	1
<i>Asaphidion flavipes</i>	4	2	3	1
<i>Badister bullatus</i>	6	3	3	1
<i>Badister sodalis</i>	4	3	1	1
<i>Bembidion guttula</i>	3	3	3	1
<i>Bembidion lampros</i>	4	2	3	1
<i>Bembidion mannerheimii</i>	3	3	1	1
<i>Bembidion obtusum</i>	3	2	3	1

Table A1. Continued.

Species	Body size	Category	Flight ability	Trophic level
<i>Bembidion properans</i>	4	3	3	1
<i>Bembidion quadrimaculatum</i>	3	2	3	1
<i>Bembidion quinquestriatum</i>	5	3	3	1
<i>Bembidion tetracolum</i>	6	2	3	1
<i>Brachinus crepitans</i>	8	1	2	1
<i>Bradycellus harpalinus</i>	4	1	3	1
<i>Bradycellus verbasci</i>	4	2	3	1
<i>Calathus ambiguus</i>	10	1	3	1
<i>Calathus cinctus</i>	8	1	3	1
<i>Calathus fuscipes</i>	12	2	1	1
<i>Calathus melanocephalus</i>	7	2	2	1
<i>Calathus micropterus</i>	8	3	1	1
<i>Callistus lunatus</i>	7	1	2	1
<i>Calodromius spilotus</i>	4	3	3	1
<i>Carabus auratus</i>	24	2	1	1
<i>Carabus auronitens</i>	22	3	1	1
<i>Carabus cancellatus</i>	22	2	1	1
<i>Carabus clatratus</i>	25	3	3	1
<i>Carabus convexus</i>	17	1	1	1
<i>Carabus coriaceus</i>	34	3	1	1
<i>Carabus granulatus</i>	19	3	1	1
<i>Carabus monilis</i>	24	3	1	1
<i>Carabus nemoralis</i>	26	3	1	1
<i>Carabus problematicus</i>	24	3	1	1
<i>Carabus violaceus</i>	27	3	1	1
<i>Chlaenius nigricornis</i>	11	3	3	1
<i>Cicindela campestris</i>	13	2	3	1
<i>Clivina fossor</i>	6	2	3	1
<i>Cychrus attenuatus</i>	17	3	1	1
<i>Cychrus caraboides</i>	17	3	1	1
<i>Cylindera germanica</i>	10	2	1	1
<i>Cymindis axillaris</i>	9	1	2	1
<i>Cymindis humeralis</i>	9	1	1	1
<i>Demetrias atricapillus</i>	5	3	3	1
<i>Dromius quadrimaculatus</i>	6	3	3	1
<i>Dyschirius globosus</i>	2	3	2	1
<i>Elaphrus cupreus</i>	8	3	3	1
<i>Harpalus affinis</i>	9	2	3	1
<i>Harpalus anxius</i>	7	1	3	3
<i>Harpalus atratus</i>	11	1	2	3
<i>Harpalus dimidiatus</i>	13	1	2	3
<i>Harpalus honestus</i>	9	1	2	3

Table A1. Continued.

Species	Body size	Category	Flight ability	Trophic level
<i>Harpalus laevipes</i>	11	3	3	3
<i>Harpalus latus</i>	9	2	3	3
<i>Harpalus rubripes</i>	10	2	3	3
<i>Harpalus rufipalpis</i>	9	1	3	3
<i>Harpalus schaubbergerianus</i>	9	1	3	3
<i>Harpalus signaticornis</i>	6	1	2	3
<i>Harpalus smaragdinus</i>	10	1	3	3
<i>Harpalus tardus</i>	9	2	3	3
<i>Harpalus tenebrosus</i>	10	1	3	3
<i>Laemostenus terricola</i>	15	2	1	1
<i>Lebia chlorocephala</i>	6	3	3	1
<i>Lebia cruxminor</i>	6	1	3	1
<i>Leistus ferrugineus</i>	6	2	1	1
<i>Leistus spinibarbis</i>	9	2	2	1
<i>Loricera pilicornis</i>	8	3	3	1
<i>Microlestes maurus</i>	2	1	2	1
<i>Microlestes minutulus</i>	3	1	3	1
<i>Molops elatus</i>	16	3	1	1
<i>Molops piceus</i>	13	3	1	1
<i>Nebria brevicollis</i>	11	2	3	1
<i>Nebria salina</i>	11	1	3	1
<i>Notiophilus aquaticus</i>	5	2	3	1
<i>Notiophilus biguttatus</i>	5	3	3	1
<i>Notiophilus germinyi</i>	5	2	2	1
<i>Notiophilus palustris</i>	5	3	3	1
<i>Notiophilus rufipes</i>	5	3	3	1
<i>Notiophilus substriatus</i>	5	2	3	1
<i>Ophonus ardosiacus</i>	11	1	2	3
<i>Ophonus azureus</i>	7	1	3	3
<i>Ophonus melletii</i>	7	1	3	3
<i>Ophonus nitidulus</i>	10	1	3	3
<i>Ophonus parallelus</i>	7	1	2	3
<i>Ophonus puncticeps</i>	8	1	3	3
<i>Ophonus puncticollis</i>	7	1	3	3
<i>Ophonus rufibarbis</i>	7	2	3	3
<i>Panagaeus bipustulatus</i>	7	1	2	1
<i>Paradromius linearis</i>	4	2	2	1
<i>Parophonus maculicornis</i>	6	1	2	3
<i>Philorhizus melanocephalus</i>	3	2	3	1
<i>Philorhizus notatus</i>	3	1	2	1
<i>Poecilus cupreus</i>	12	3	3	1
<i>Poecilus lepidus</i>	12	1	1	1

Table A1. *Continued.*

Species	Body size	Category	Flight ability	Trophic level
<i>Poecilus versicolor</i>	11	2	3	1
<i>Pseudoophonus rufipes</i>	14	2	3	3
<i>Pterostichus longicollis</i>	6	3	2	1
<i>Pterostichus madidus</i>	15	3	1	1
<i>Pterostichus melanarius</i>	15	2	3	1
<i>Pterostichus niger</i>	19	3	3	1
<i>Pterostichus nigrita</i>	10	3	3	1
<i>Pterostichus oblongopunctatus</i>	11	3	2	1
<i>Pterostichus ovoideus</i>	7	2	1	1
<i>Pterostichus rhaeticus</i>	10	3	3	1
<i>Pterostichus strenuus</i>	6	2	3	1
<i>Pterostichus vernalis</i>	7	3	3	1
<i>Stomis pumicatus</i>	7	3	1	1
<i>Syntomus foveatus</i>	3	1	3	1
<i>Syntomus truncatellus</i>	3	1	3	1
<i>Synuchus vivalis</i>	7	2	2	1
<i>Trechus obtusus</i>	4	2	3	1
<i>Trechus quadristriatus</i>	4	2	3	1
<i>Trichotichnus laevicollis</i>	7	3	1	1
<i>Trichotichnus nitens</i>	8	3	1	1
<i>Zabrus tenebrioides</i>	14	2	3	3

Appendix 3

Table A2. AIC scores for the generalized linear mixed models of species richness per habitat preference group. Dataset was included as a random variable in all models. The best three models within 15 AIC points of the best model are given in bold. The pattern of AIC scores was identical for activity density (natural log transformed).

Model	Dry grassland	Generalist	Forest & wet grassland
.	244.9	448.2	685.4
Area	238.2	449.4	687.1
Area + 500m	230.9	437.6	686.1
Area + 1000m	234.7	446.8	685.8
Area * trophic level	130.8	182.4	149.6
Area * trophic level + 500m	123.1	170.5	148.5
Area * trophic level+ 1000m	127.5	179.9	148.3

Appendix 4

Table A3. Model averages for the fixed effects parameters in the best three generalized linear mixed models for activity density (natural log scale) per habitat affinity group. Significant effects are marked: * $p < 0.05$, ** $p < 0.01$.

Fixed effect	Estimate	Std. Error	z value	p
<i>Dry grassland</i>				
(Intercept)	-4.17339	1.30855	-3.188	0.002**
Area	0.45206	0.12044	3.753	<0.001**
Trophic level shift	-0.34450	2.84219	-0.121	0.904
Phytophagous	5.65831	1.41822	3.989	<0.001**
Area * Trophic level shift	-0.12237	0.26767	-0.457	0.648
Area * Phytophagous	-0.49899	0.13455	-3.708	<0.001**
Additional calc. grass. 500m	0.02512	0.01551	1.620	0.105
Additional calc. grass. 1000m	0.02090	0.01543	1.354	0.176
<i>Generalist</i>				
(Intercept)	0.57947	0.47250	1.235	0.260
Area	0.07121	0.04156	1.712	0.096
Trophic level shift	-0.48149	0.82524	-0.584	0.560
Phytophagous	0.47163	0.68359	0.690	0.490
Area * Trophic level shift	-0.06701	0.07679	-0.873	0.383
Area * Phytophagous	-0.10815	0.06397	-1.690	0.091
Additional calc. grass. 500m	0.03359	0.01047	3.209	0.001**
Additional calc. grass. 1000m	0.02625	0.01027	2.557	0.011*
<i>Forest & wet grassland</i>				
(Intercept)	0.61987	0.49592	1.258	0.234
Area	0.07720	0.04367	1.767	0.082
Trophic level shift	-1.10087	1.19834	-0.919	0.358
Phytophagous	0.20281	0.81556	0.249	0.804
Area * Trophic level shift	-0.09551	0.11373	-0.840	0.401
Area * Phytophagous	-0.13254	0.07773	-1.705	0.088
Additional calc. grass. 500m	0.02071	0.01126	1.839	0.066
Additional calc. grass. 1000m	0.02402	0.01114	2.156	0.031*

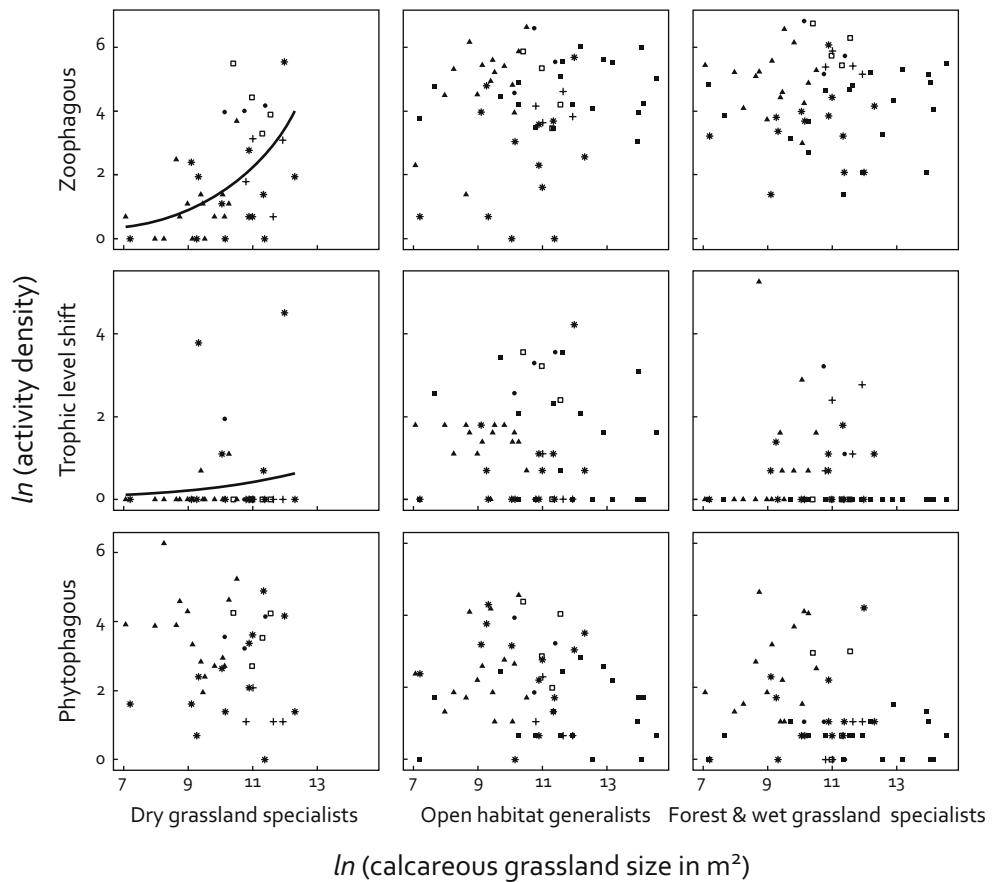
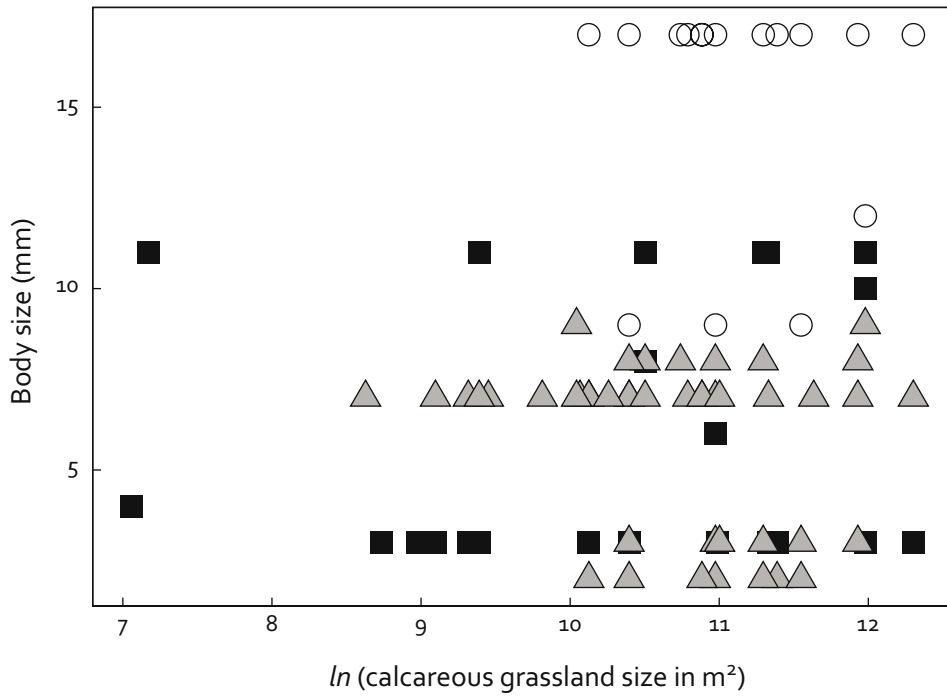


Figure A2. Activity density (natural log scale) of zoophagous species (upper panels), phytophagous species with zoophagous larvae (middle panels) and phytophagous species (lower panels) as a function of calcareous grassland size (natural log scale). Species are grouped by habitat affinity: typical dry grassland species (left), generalist open habitat species (middle) and wet grassland and forest species (right). Fitted lines (Poisson GLMM) are plotted where significant effects of calcareous grassland size on activity density (natural log scale) were found (see Table appendix 3).

Appendix 5





Nest of Polistes spec. on a newly restored calcareous grassland (Photo: Toos van Noordwijk)

Chapter 8

Synthesis

C.G.E. (Toos) van Noordwijk

The aim of this thesis is to gain knowledge at three distinct levels. Firstly, to develop tools that provide mechanistic understanding of species-environment relationships. Secondly, to increase our general understanding of species-environment relationships, i.e. why are species limited to specific sites. Thirdly, to provide applied management advice to conserve arthropods in calcareous grasslands. Specifically, my research questions are:

- 1) To what extent have arthropod communities in Dutch calcareous grasslands been restored over the past two decades of conservation management?
- 2) How can species' traits and their interactions be used to gain insight in the mechanisms underlying species-environment relationships?
- 3) How are arthropods in calcareous grasslands affected by environmental stressors, in particular isolation, fragmentation, vegetation structure & microclimate and disturbance caused by grassland management?
- 4) Which strategies are most effective to restore and conserve arthropod communities in Dutch calcareous grasslands?

In this chapter, I will synthesize the knowledge gained in chapters 2-7 at each of these three levels. I start by evaluating to what extent the arthropod communities in Dutch calcareous grasslands have been restored over the past two decades of conservation management. Next, I explore what type of information we need to gain mechanistic understanding of why species are limited to specific sites. This is followed by a discussion of alternative approaches to use traits and trait interactions to unravel such species-environment relationships. Then, I summarize the new insights my research has provided with respect to general species-environment relationships. Finally, I discuss what this all means for arthropod conservation in (Dutch) calcareous grasslands.

Changes in arthropod communities following renewed conservation management

Arthropod communities in calcareous grasslands in Northwestern Europe have been severely degraded during the 20th century, due to land-use change, eutrophication, abandonment and fragmentation (Willems 2001; Poschlod and WallisDeVries 2002; WallisDeVries et al. 2002). Over the past decades, increased efforts have been made to conserve remaining sites and to restore degraded calcareous grasslands. This is most commonly done through grazing or mowing management (Bobbink and Willems 1993; Willems 2001). Arthropod communities found under varying management regimes have been studied since the 1970s (e.g. Morris 1973, 1979; Morris and Rispin 1988). These studies indicated that many specialist arthropods are very sensitive to disturbances caused by grazing and mowing management, even though some form of management is vital for their long-term persistence. Surprisingly, changes in arthropod diversity or composition over time following renewed conservation management have rarely been studied. Where such data exist, for example from long term butterfly monitoring schemes, results are mixed. For example, butterfly monitoring data in the UK showed that renewed conservation management led to increased abundances of some focal species, but others continued to decline (Bourn and Thomas 2002). In Dutch calcareous grasslands, all characteristic calcareous grassland butterflies continued to decline, even after specific management strategies had been implemented (WallisDeVries et al. 2002). To gain better understanding of the effects of renewed management on a wide range of arthropod taxa, I compared pitfall trap data collected in 1988 and 2005 in eight calcareous grasslands in the province of Zuid-Limburg (chapter 2). For all seven investigated arthropod groups I found considerable species turn-over (i.e. the species list per site differed considerably between the two sampling years). However, overall patterns differed markedly between taxonomic groups. Only for spiders I found a significantly greater increase in occurrence for characteristic calcareous grassland species than for generalist species. Carabid beetle species richness declined in spite of conservation efforts. At the same time species richness of true bugs and millipedes increased, while spiders, ants, weevils and woodlice did not show significant changes in species richness. Also at the regional scale, effects of management on diversity patterns were mixed. Communities of carabid beetles and weevils became more similar across calcareous grasslands in Zuid-Limburg (biotic homogenization). In contrast, compositional variation among sites increased for millipedes (differentiation). These results indicate that the renewed management, which consisted of grazing or mowing, mostly executed in autumn, has had some positive effects. However, it has not led to full recovery of arthropod communities and some groups even continued to decline. This highlights the need to identify remaining bottlenecks and to devise management strategies to tackle them.

From patterns to processes

Traditionally, research into the importance of particular stressors for entire communities has strongly relied on correlative techniques (McGill et al. 2006). However, inferring causal relationships from current occurrence patterns can be misleading, as they do not automatically imply causality (see Box 1). Predicting which management regimes address current bottlenecks thus requires understanding of the underlying mechanisms. Traits have been proposed as a fruitful tool for community ecology, providing such mechanistic understanding of species responses to environmental gradients (Keddy 1992; McGill et al. 2006; Vandewalle et al. 2010).

Most commonly, traits have been used as independent predictors of a species' ability to deal with particular environmental conditions (Keddy 1992; McGill et al. 2006; Webb et al. 2010). In chapter 2 I also used traits and other species' characteristics as

Box 1. A seemingly strong correlation between bug and beetle richness

How correlation does not automatically imply causality

Comparison of the carabid beetle data and ground dwelling true bug data in eight calcareous grasslands in 2005 (see chapter 2) revealed that the species richness of these two groups was strongly correlated (Figure 1 (right)). $\text{lm: } t = 2.90, R^2 = 0.52, P = 0.027$). This concordance between groups would indicate that one group can be used as a surrogate for the other, greatly facilitating future biodiversity inventories. However, correlating the species richness of the same taxonomic groups from the same sites sampled with the same method in 1988 reveals a very different pattern (Figure 1 (left)). There is no longer a significant correlation between richness patterns of these two groups ($\text{lm: } t = -0.62, R^2 = -0.09, p = 0.56$) and the site with the highest carabid beetle richness even harbours the lowest number of true bug species. While carabid species richness declined between 1988 and 2005, species richness of true bugs increased. These contrasting temporal trends suggest that the richness patterns found for these two groups in 1988 and 2005 are caused by different mechanisms.

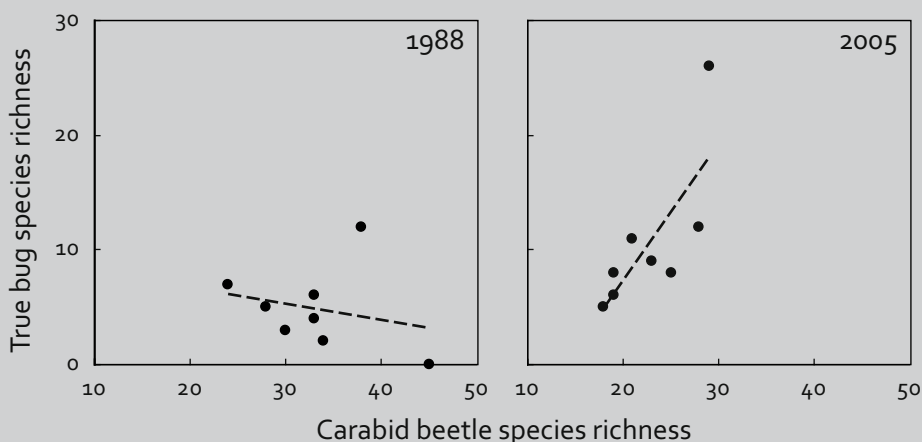


Figure 1. Species richness of ground dwelling true bugs and carabid beetles per calcareous grassland site in 1988 (left) and 2005 (right). Richness was assessed with two pitfall trap series per site, operated from April to October (see chapter 2 for a more detailed methods description).

independent predictors, investigating whether temporal changes in species' occurrence patterns differed according to species' dispersal ability, habitat specialization, food specialization and trophic level. Indeed, some of the variation in occurrence patterns was explained by these traits and characteristics. However, results were not consistent across taxonomic groups and the explanatory power was generally low. There are two main reasons for this lack of explanatory power. Firstly, as discussed in chapter 1, natural selection does not operate on single traits, but on individuals. An individual's fitness in a specific environment is determined by the combined effect of its traits (Siepel 1994; Verberk et al. 2013). This means that the adaptive value of a specific trait may depend on other traits possessed by that individual (see examples given in chapter 1). Secondly, trait-environment research has generally focussed on the effect of specific environmental gradients (Keddy 1992; McGill et al. 2006), e.g. land-use intensity (Ribera et al. 2001), extreme winter warming (Bokhorst et al. 2011) or environmental disturbance (Williams et al. 2010). In semi-natural habitats undergoing renewed conservation management, however, many different factors operate simultaneously, which all affect the local species composition. For example, the local species composition may be simultaneously altered by changes in vegetation structure, changes in disturbance regime, changes in microclimate due to climate change and ongoing effects of habitat isolation and fragmentation. In addition, these factors may differently affect different trophic levels, altering biotic interactions. This multitude of stressors can be expected to cause a multitude of responses both within and between taxonomic groups. To gain understanding of the causes of decline and possibilities for restoration of arthropod communities in calcareous grasslands, we thus need an approach that incorporates trait interactions and enables disentangling the effects of multiple stressors. Below I will explore methods to tackle these issues from the species-end, using life-history strategies and from the environment end of species-environment relationships.

Using life-history strategies to unravel species-environment relationships

Life-history strategies have been presented as a particularly suitable method to incorporate trait interactions and to disentangle the effects of multiple stressors on a community. Following the assembly filter concept (see chapter 1, figure 2), species currently present in the local species pool can be viewed as the combined result of the filters operating on a site (Webb et al. 2010). Only species whose life-history enables them to cope with all environmental conditions simultaneously, will be able to persist. This implies that analyzing the life-history of the species currently present at a site can be used to deduce which aspects of the habitat have shaped the current community. This concept has been operationalized through the use of life-history strategies or tactics (Siepel 1994; Verberk et al. 2008a, 2013). In this approach species' traits related to the four domains of reproduction, development, dispersal and synchronization are listed and the adaptive value of these trait combinations is deduced from literature. Considering a species' adaptations in all four domains simultaneously reveals trait interactions, such as trade-offs in resource allocation, spin-offs (investment in one trait favours investment in another trait) or constraints (investment in one trait makes it physically impossible to possess another trait). In addition to such internal trait interactions (i.e. tied together by a species

energy balance or body plan constraints), traits can also interact by influencing each other's ecological consequences. Specific combinations of trait attributes can make species vulnerable to specific stressors, while each trait separately has no adverse effects. For example, in noctuid moths, body size, larval food specificity and flight period length were found to have no effect on species' distribution changes in Finland (Mattila et al. 2006). However, taken together, large bodied species with short flight periods and monophagous caterpillars proved to have much higher extinction risks than other species. Taking all traits and trait interactions together reveals to which circumstances a species is well adapted. Species can then be grouped accordingly, resulting in life-history strategies that respond similarly to changes in their environment. In chapter 3, I applied this life-history strategy approach to ants. This revealed three particular circumstances to which ants are vulnerable, two of which seem limiting in Dutch calcareous grasslands: habitat isolation and microclimatic conditions in summer.

The strength of the life-history strategy approach is that it explicitly incorporates trait interactions. It allows to evaluate the relative importance of traits and to weight traits in an informed way, depending on the remainder of a species' biology (Verberk et al. 2013). For example, in chapter 3 I revealed that the extent to which ant species depend on warm microclimatic conditions depends on the combined effect of several traits relating to colony founding behaviour and larval development. The time constraint for larval development, causing species to be limited to nest founding sites with warm microclimates, only arises for species with claustral colony founding (queens feeding their first batch of workers from their own fat reserves). Other species can replenish their food reserves by foraging, giving them ample time for development, irrespective of their other colony founding and development traits. Thus, traits related to development and the timing of colony founding are only relevant for an ant species' vulnerability to cold microclimates for ants with a specific nest founding mode. Consideration of internal trait interactions (i.e. trade-offs, spin-offs and constraints) in the life-history strategy approach also highlights that an adaptation to specific conditions usually makes a species less adapted to other circumstances. For example, in ants, claustral nest founding makes ant species less vulnerable to food shortages (as single queens don't have to forage), but in return increases their dependence on warm microclimatic conditions (see chapter 3).

The life-history strategy approach is explicitly mechanistic. This allows results to be extrapolated to other (similar) species or circumstances. The strategies developed for ants in calcareous grasslands could be applied to dunes or heathlands. These sites are likely to contain some additional species, but these can be assigned to existing strategies based on their traits. Even species with trait attributes not found in calcareous grasslands may be assigned to existing strategies if they have similar ecological consequences.

A third important advantage of the life-history strategy approach is that it draws attention to very specific bottlenecks for the species group under study. In chapter 3 we demonstrated that specifically soil temperature in summer and early autumn is an important parameter for ants in chalk grasslands, rather than soil temperature in general. This led to the specific hypothesis that summer management is essential, which was confirmed by subsequent analysis of field data. Multivariate comparisons of single-trait data would likely have overlooked this factor as no single trait governs a species'

vulnerability to summer soil temperature and researchers would have measured soil temperature with no specific timing.

In spite of these clear advantages over single trait approaches, the life-history strategy approach has been criticized. In particular, criticism has focused on the following three points. First, it requires extensive knowledge of a species' biology. Second, there are no fixed guidelines for the adaptive value of a specific trait. Third, there is no fixed level of aggregation (Verberk 2008; Van Turnhout 2011). Indeed the compilation of strategies requires extensive knowledge of a species' biology and of the adaptive value of specific trait combinations. This is problematic for some arthropod groups, including even well studied taxa like carabid beetles. Often, little knowledge is available on the development of immature stages, while these are likely to be the most vulnerable life-cycle stage (Thiele 1977; see also chapter 7).

The second point of criticism is the lack of fixed adaptive values of specific trait attributes. For example in chapter 3, I only evaluated a species' development speed for claustral species. Such different weighing of traits depending on the remainder of a species biology is often regarded as making the compilation of life-history strategies arbitrary, lacking scientific rigor. However, ignoring the context dependence of trait values and presenting traits as fixed values is arguably more arbitrary (see also Verberk et al. 2013). Recall, for example, the relationship between body-size and dispersal ability in carabid beetles (see chapter 1). While body-size is often positively associated with dispersal ability, for example in bees (Steffan-Dewenter and Tscharrntke 1999), this does not hold true for carabid beetles. Large-bodied carabid species are generally flightless (Turin 2000). Thus although large-bodied carabid species can often run faster than small-bodied species, their overall dispersal ability is lower because they cannot fly. Body-size thus sometimes correlates with dispersal behaviour, but not in all cases, i.e. the adaptive value of the trait body-size depends on the remainder of a species' biology. Of course, without fixed trait values (e.g. body-size being a proxy for dispersal ability in some species, but having a different adaptive value in other species) there are no boundaries to the imagination. Any far fetched hypothesis on the adaptive value of specific trait combinations can be compiled. However, this is not necessarily a problem, as long as hypotheses are firmly rooted in logic combinations of existing biological knowledge. Moreover, derived hypotheses should subsequently be put under scrutiny through rigorous testing of field data (see chapter 3). In fact, new hypotheses on the adaptive value of specific trait combinations are essential to derive new insights into the bottlenecks species are encountering in their environments. Without new hypotheses on the adaptive value of various nest founding modes, I would not have uncovered summer soil temperature as a specific bottleneck for some ant species (see chapter 3).

The objection that there is no fixed level of aggregation for life-history strategies is perhaps the most legitimate criticism. Life-history strategies have generally been presented as fixed entities that can be applied in any context (Siepel 1994; Verberk et al. 2008a). However, within each group, species are adapted to slightly different circumstances. In this respect the term 'life-history strategy' (or tactic as it was called by Stearns (1976) and Siepel (1994)) is confusing. It refers both to the entire life-cycle of a single species (*sensu* Stearns (1976)) and to the ecological consequences with respect to a specific set

of environmental conditions (*sensu* Siepel (1994)). Species with different life-cycles, and hence different life-history strategies *sensu* Stearns, may respond similarly to their environment and hence have the same life-history strategy *sensu* Siepel. For example, in chapter 3, I assigned species with parasitic nest founding and nestfounding through nest-splitting (thus different reproductive strategies) to the same life-history strategy, as both life-cycles cause species to have a limited dispersal ability. To be unambiguous it would be better to refer to the latter use, i.e. groups of species that respond in a similar way to their environment (but do not necessarily have the exact same trait attributes), as *ecological* strategies. If we would include all possible traits each species would be assigned to a separate ecological strategy. This, of course, serves no purpose as it does not help to make any generalizations and does not improve predictive power. We thus need to choose an intermediate level of abstraction that includes main traits, but excludes minor differences between species. Choosing which traits to include is to some extent subjective, as there is no single objective level of aggregation above the species level. However, the fact that there is no single fully objective level of aggregation that suits *all* ecological questions, does not mean that there are no appropriate levels of aggregation for *specific* ecological questions. For example, ants are generally well adapted to cope with many aspects of their environment by forming colonies with division of labour (Hölldobler and Wilson 1990). This makes the stage at which new colonies are formed especially vulnerable (Hölldobler and Wilson 1990), causing the solution species have evolved to cope with colony formation to bear great implications for their survival under different environmental conditions. For ants, all traits related to colony founding thus form a natural level of aggregation for strategies.

Exploring environmental filters

Most trait research so far has not started at the species end of species-environment relationships, but rather investigated a single ecological gradient or stressor (Keddy 1992; McGill et al. 2006). This bypasses the difficulties of having to disentangle different environmental stressors from the traits of species present in the local species pool. A natural draw-back is that only stressors which are already deemed important will be investigated, hampering the discovery of new bottlenecks (like summer soil temperature in chapter 3). Nonetheless, many potential stressors, including habitat isolation and fragmentation, have already been identified to affect local communities, warranting further investigation into their impact. In chapter 7, I used this approach to investigate how the importance of calcareous grassland area depends on the trophic rank, habitat affinity and dispersal ability of carabid beetles. All three traits and species characteristics had previously been associated with vulnerability to habitat size, but empirical evidence so far was inconclusive (Steffan-Dewenter and Tscharncke 2002; Henle et al. 2004; Van Nouhuys 2005). My analysis demonstrated that trophic level, habitat affinity and dispersal ability synergistically affect species' sensitivity to habitat area. While each trait independently had low predictive power, together they show a clear pattern. Only carabid beetles that were both zoophagous *and* characteristic for calcareous grasslands responded strongly to calcareous grassland area, especially if they had poor dispersal ability. Thus also when investigating single environmental factors, (in this case habitat size), it is crucial to incorporate trait interactions. This has previously been demonstrated,

e.g. by Öckinger et al. (2010) who showed that the response of butterflies and moths to habitat area and isolation depends on the combined effect of niche breadth, reproductive potential and dispersal ability. Similarly, Davies et al. (2004) highlighted that the response of beetles to fragmentation depends on the synergistic effect of their natural abundance and level of specialisation.

An advantage of starting at the environment end of species-environment relationships is that the specific stressor under study gives clear guidelines as to the circumstances to which adaptations are needed. This focuses the search for relevant traits and adaptations and makes it unnecessary to investigate a species' entire life-history. While being a great advantage, this clear focus also holds a potential risk. Analyses will generally be limited to the 'usual suspects' (e.g. flight ability when studying dispersal or drought resistance when studying responses to climate change). However, seemingly unrelated traits may alter species' responses as well. For example, in chapter 6 it was demonstrated that a species' spread rate through fragmented landscapes is not only affected by a species' dispersal traits but also by its traits related to reproduction and development, e.g. age at maturity and reproductive rate. Also, trait research in arthropods has so far strongly focussed on adult life stages (e.g. Ribera et al. 2001; Vanbergen et al. 2010), while immature stages are often less mobile and more vulnerable to unfavourable conditions (Thiele 1977; Bourn and Thomas 2002; chapter 5).

Through arthropod eyes

Ultimately, understanding the match between species' life-cycles and environmental assembly filters requires knowledge of both. This means that the two approaches described above, i.e. the ecological strategy approach and the exploration of environmental filters, should ideally be integrated into one iterative process. A fruitful way to do this is to view the environment 'through an arthropod's eyes', much in the same way as the 'Umwelt' – concept advocated by Van Dyck (2012). The key to this concept is to realize that different organisms live in different perceptual worlds (Van Dyck 2012). Analysing a species' life-cycle and comparing each stage against the environment in which it occurs, highlights both the challenges that must be overcome and to what extent the species has trait attributes to do so (see Box 2). In essence this approach is similar to the construction of ecological strategies (better known as life-history strategies or tactics), but it is more flexible. The strategy approach uses life-history traits in the four domains of reproduction, development, dispersal and synchronization as its backbone. This covers the main areas of energy expenditure and presents a consistent intermediate level between underlying morphological, physiological and phenological (MPP) traits and resulting behavioral adaptations (e.g. level of food specialization and nest location). Only using life-history traits, dismisses information at the MPP trait level and the behavioural response level, which may give valuable additional information, if associated life-history traits are unknown. For example, in butterflies life-history traits like the number and size of eggs produced per female, are linked to a species' behavioural responses such as larval food plant specialization and adult feeding behaviour. Species specializing on larval food plants of poor nutritional quality, or with rarely feeding adult stages, have less energy in total to spend on reproductive output than species with both feeding adults and high quality

Box 2. Viewing the landscape through arthropod eyes

Evaluating a species' life-cycle against the landscape in which it occurs is a fruitful approach to gain insight in potential bottlenecks. In Figure 2, the life-cycle of characteristic calcareous grassland butterflies (e.g. the Glanville fritillary, *Melitaea cinxia*) is compared against Dutch calcareous grasslands with autumn management. Autumn management provides an open vegetation structure in early spring that creates a warm microclimate for basking caterpillars and sufficient fresh regrowth of the larval food plant (*Plantago lanceolata*). In early summer, during the adult flight season, the site provides ample food for adult butterflies and larval food plants for egg-laying. However, in autumn, sites are grazed to a very short turf height. This provides very little shelter for hibernating caterpillars and may therefore hamper larval survival. Several traits and characteristics determine how prone species are to this potential bottleneck. These include hibernation stage, hibernation location (in the soil, on the ground or in the vegetation layer), the number of generations per year (affecting a species' ability to compensate high winter mortality rates) and whether species are restricted to calcareous grasslands. This analysis led to the hypotheses tested in chapter 5.

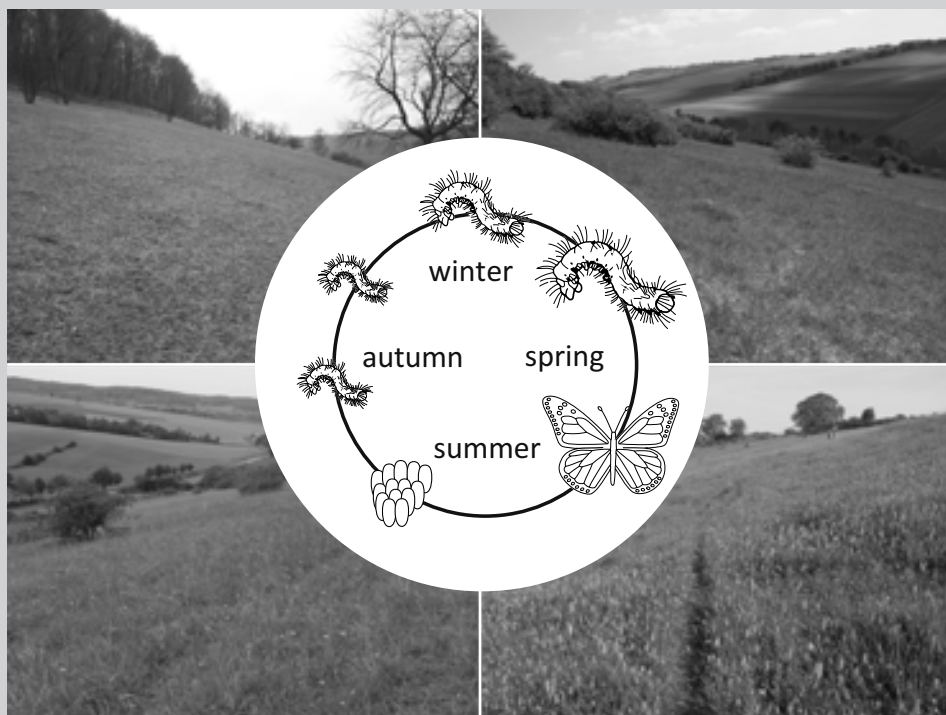


Figure 2. Comparing the life-cycle of calcareous grassland butterflies against Dutch calcareous grasslands.

larval food plants (Bink 1992). Species' characteristics like food plant specialization and adult feeding behaviour are generally better known than the associated life-history traits. Thus, going through a species' life-cycle, using all available information, may give a more accurate understanding of the challenges it encounters than strictly following the strategy approach. A particularly useful application is to compare life cycles of declining species with those of closely related species that perform better, in order to identify the crucial part of the life-history that causes these differences (Kotiaho et al. 2004; Van Turnhout et al. 2010).

Understanding a species' entire life-history and all its ecological consequences undoubtedly gives the most accurate mechanistic understanding and thus allows best to predict species' responses to environmental stressors. However, it has been rightfully questioned whether we have enough knowledge of species' traits and enough understanding of their ecological consequences to do so. Moreover the existence of fixed ecological strategies, i.e. groups of species that respond similarly to all aspects of their environment, may be a myth. As acknowledged by Verberk (2008) and Verberk et al. (2013), the level of aggregation of ecological strategies should be adjusted to the specific research question, the range of interspecific biological variation and the availability of trait information. Therefore, evaluating species' life-cycles in relation to specific environmental stressors may be more effective than grouping species into fixed ecological strategies. This does not mean that there are no general patterns. As highlighted above, species-environment relationships found for a specific set of species in a specific environment can be extrapolated to other species or circumstances (e.g. using the strategies compiled in chapter 3 for ants in dunes). However, there is no single limited set of traits that explains the presence or absence of a set of species under all circumstances. Researchers should therefore evaluate critically whether pre-existing classifications are relevant in the light of their particular research question.

Systematically analyzing an arthropod's life-cycle in the way described above has several advantages. Like the strategy approach, it draws attention to trait interactions (as the entire life-cycle is evaluated) and it explicitly incorporates immature stages. In addition, this approach allows to use all available knowledge on various levels (MPP traits, life-history traits and behavioural responses). The main pitfall is that it lacks a fixed structure and may lead to unfounded, descriptive studies that bear little predictive power. To gain structure, the aim of finding mechanistic understanding and to retrieve testable hypotheses should be used as a 'compass' to guide which information to incorporate in the life-cycle analyses. For example, a species' dispersal ability can be deduced from the combined effect of multiple traits such as wing size, wing development, walking speed and dispersal behaviour. Alternatively, dispersal ability can be directly measured as the maximum displacement in m/hour. Although studying such a single overarching trait effectively resolves some of the difficulties presented by trait interactions, it generally reduces mechanistic understanding. In the case of dispersal ability, flightless, fast walking carabid beetles may score similarly to small flying species in direct dispersal speed measurements. However, their performance becomes very different when confronted with a waterway. This can be predicted from the set of traits that incorporates the movement mechanism (walking or flying) in addition to the movement speed. Such mechanistic understanding is not provided by the single direct measurement of dispersal speed. Thus, incorporating

the detailed traits and their interactions greatly improves mechanistic understanding (Verberk et al. 2013) and should thus be preferred.

To gain predictive power, life-cycles should be compared between species. In line with the strategy approach species can then be grouped according to their predicted response to the specific environmental stressor(s) under study. Hypotheses derived from such life-cycle analyses should then be rigorously tested before further implementation.

Advancements in species-environment relationships

Using the various methods discussed above, the research presented in this thesis has revealed several new insights in species-environment relationships. In chapter 3, it was discovered that microclimatic conditions are particularly important for ant species exhibiting claustral colony founding (i.e. with queens feeding the first batch of workers from their own fat reserves). Soil temperatures are however only limiting for species that are constrained in their development time due the combined effect of a number of traits relating to colony founding behavior and larval development. For these species specifically the soil temperature in summer and autumn is crucial for colony founding. In chapter 4 a literature review was carried out to summarize all known effects of grazing on arthropod diversity. This revealed that arthropod species richness is generally more sensitive to grazing than plant species richness. In chapter 5, it was demonstrated experimentally that autumn and winter grazing can pose a serious threat to hibernating butterfly larvae. Grazing intensity seems to be an important factor determining larval mortality rates. Chapter 6 highlighted that species persistence and dispersal in fragmented landscapes does not only depend on dispersal traits, but also on population vital rates, like age at maturity and carrying capacity. In chapter 7, it was demonstrated that trophic level, habitat affinity and dispersal ability synergistically affect species' sensitivity to habitat area. In addition, this study indicates that the effect of trophic level is independent of a species degree of food specialization. Therefore, the effect of habitat fragmentation on trophic interactions may be greater than previously anticipated. In all, these results demonstrate that effective conservation of arthropod communities calls for both optimization of the management regime within calcareous grassland reserves and addressing issues of habitat isolation and fragmentation in the wider landscape. Specific management recommendations for (Dutch) calcareous grasslands are discussed below.

Management of calcareous grasslands

Management in the form of grazing or mowing is essential to conserve species-rich calcareous grasslands on the long run. Insufficient management leads to a dense, homogeneous vegetation structure, a loss of characteristic plant species and a cool and wet microclimate (Willems 2001; WallisDeVries et al. 2002). Too intensive management is also detrimental for arthropod species richness (Morris et al. 1990; Mortimer et al. 1998; Morris 2000), as the availability of food and shelter decreases and direct disturbance increases (chapter 4 and 5). The current management regime in most Dutch calcareous grasslands, consisting of intensive grazing or mowing in autumn, has proven to be too intensive for some arthropods and too extensive for others. It is insufficient to create

an open vegetation structure and warm microclimate in summer for characteristic ant species (chapter 3) and it leads to high mortality rates among overwintering caterpillars (chapter 5). Smits (2010) demonstrated that this management regime also leads to insufficient nutrient removal, hampering the recovery of characteristic plant species. These bottlenecks can all be addressed by shifting the main management period to late spring or early summer. This will increase soil temperatures in late summer and decrease disturbance caused by grazing animals to hibernating caterpillars. Also nutrient removal is likely to be more effective in summer than in autumn (Bobbink and Willems 1991; Smits et al. 2009). Some reserves are already grazed in summer with positive effects, at least for the microclimatic conditions and the presence of characteristic ant species (chapter 3). However, summer management may cause new bottlenecks. Food sources for pollinators will be depleted and characteristic plant species will be consumed before seed set. These issues can be alleviated by spreading the management intensity in time and space. A rotational grazing regime that allows sufficient vegetation regrowth between grazing rounds, seems most effective to restore both plant and arthropod diversity (chapter 4). Field trials are necessary to ascertain the effectiveness of this grazing regime for biodiversity conservation. Such trials are currently undertaken in a number of Dutch calcareous grasslands.

A rotational grazing regime is likely to improve arthropod biodiversity and specifically survival chances for characteristic calcareous grassland arthropods. However, full recovery seems impossible under current nutrient levels. These nutrient levels are a consequence of high nitrogen deposition levels and accumulated soil nutrients due to past abandonment (Smits 2010). Their effect on plant biomass productivity may be further enhanced by climate change (Wallisdevries and Van Swaay 2006). Obtaining an optimal vegetation structure for arthropod conservation under these conditions requires intensive management. Increased grazing intensity however, quickly becomes detrimental to overall arthropod diversity (chapter 4), hampering full recovery. The only solution to this dilemma between grass and scrub encroachment, resulting from insufficient management, and too much disturbance, under more intensive management, is to drastically lower nitrogen deposition levels. Time is of the essence in this respect, because restoring arthropod populations becomes more difficult and expensive once they have been lost locally. Moreover, the backlog of nitrogen in the soil, accumulated over the past decades, means that even after atmospheric nitrogen deposition levels have been drastically reduced, (too) intensive management will still be necessary for years to come.

Habitat heterogeneity

As described in chapter 1, Box 3, many Dutch calcareous grasslands are part of a complex of dry, nutrient poor grasslands. This habitat heterogeneity adds significantly to arthropod diversity. Most species restricted to warm, nutrient poor conditions occur along the entire gradient of vegetation types, but each vegetation type also supports a number of unique species (Smits et al. 2009; Van Noordwijk et al. 2012, 2013). In addition, the variation in microclimatic conditions between these vegetation types may enable species to seek shelter from extreme conditions. Similarly, availability of calcareous grassland differing in slope and aspect in close proximity, provides a buffer against extreme weather

Box 3. Importance of habitat heterogeneity

The Glanville fritillary (*Melitaea cinxia*) was introduced in 2007 to the Winkelberg, a steep, south-facing ancient calcareous grassland (Figure 3). The population rapidly grew over the first few years (Figure 4), but numbers decreased sharply in 2011, in spite of high caterpillar numbers recorded in early spring of that year (unpublished data). The drop in butterfly numbers coincided with extremely dry and hot conditions during the adult flight season and the highest rainfall deficit ever recorded in May in the Netherlands (www.knmi.nl). Volunteers running the butterfly monitoring scheme on the Winkelberg reported extremely dry soil conditions and heavily withered vegetation (Guido Verschoor pers. comm.).



Figure 3. Aerial view of calcareous grasslands near Bemelen with ancient calcareous grassland (from left to right Strohberg and Winkelberg) shown as black hatched areas and two patches of newly developed calcareous grassland (on Verlengde Winkelberg) shown as white hatched areas (© Google Earth).

While butterfly numbers dropped at Winkelberg, butterflies and later caterpillars were first recorded on nearby sites including the newly created calcareous grassland Verlengde Winkelberg (see Figure 3). This site was created on ex-arable land in 2007 through topsoil removal and green-hay transfer (Van Noordwijk et al. 2013) on a gentle, east-facing slope. Due to these differences in aspect and inclination, and possibly differences in vegetation structure, the vegetation on Verlengde Winkelberg suffered less from the drought conditions and remained less withered (personal observations). Apparently, adult butterflies from the Winkelberg dispersed in search of more suitable habitat conditions. In autumn 2011 no caterpillar nests were found on the Winkelberg in spite of extensive searching (unpublished data) and in 2012 butterfly counts on Winkelberg were extremely low. Apparently, no more than a few individuals had survived locally. In contrast, numbers on the nearby Verlengde Winkelberg increased. In 2013 numbers on the original site, Winkelberg, increased again as well. It is unclear whether butterflies recorded on the Winkelberg

in 2012 and 2013 were offspring of local survivors or immigrants from the nearby Verlengde Winkelberg. At the very least, these data demonstrate that population trends can vary greatly between nearby sites, presumably as a consequence of differences in microclimatic conditions. The availability of alternative sites in close proximity can create a meta-population structure. This leads to increased resilience to extreme events (Hanski 1999), such as those predicted to occur more often under climate change (Thomas et al. 2004; Opdam and Wascher 2004). Especially sites differing in slope, aspect and/or vegetation structure in close proximity are likely to provide a buffer against extreme climate events.

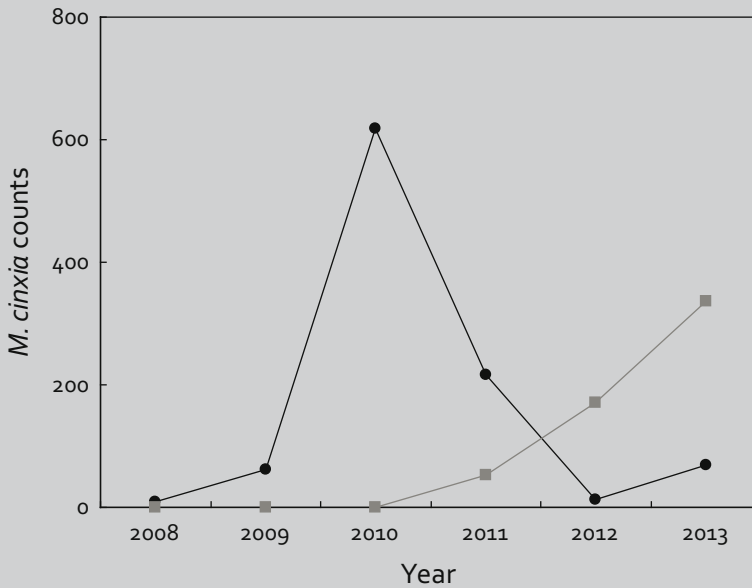


Figure 4. Number of Glanville fritillary individuals recorded per year on Winkelberg (black line) and Verlengde Winkelberg (grey line). The black line represent standardised counts of adult butterflies on monitoring routes (unpublished data NEM, De Vlinderstichting / CBS). The grey line represents caterpillar numbers counted during several site visits per year (unpublished data C.G.E. van Noordwijk and M.F. WallisDeVries).

conditions (see Box 3). Also on a smaller scale, habitat heterogeneity is essential for many characteristic arthropod species. WallisDeVries (2006) demonstrated the importance of a varied vegetation structure with bare ground and higher tufts of vegetation for the larval stages of the Glanville Fritillary (*Melitaea cinxia*). Ground nesting bees also strongly depend on patches of bare ground, in addition to floral resources (unpublished data). Management should thus strive to enhance such habitat heterogeneity by varying the management intensity within sites and by creating small scale structures, specifically patches of bare ground.

Calcareous grassland size

The largest Dutch calcareous grasslands measure just a few hectares, which is small, certainly in comparison to many sites across Europe. The landscape in Zuid-Limburg has always been characterized by small-scale heterogeneity with calcareous grasslands being restricted to the short slopes of the valleys (Hillegers 1993). Calcareous grasslands did, however, extend along most of these steep valley slopes and were thus much larger and more connected than they are today (Bobbink and Willems 2001; Knol and Schaminée 2004). Species richness generally increases with habitat area (MacArthur and Wilson 1967; Hanski 1999). Small sites can make a valuable contribution to biodiversity conservation (Tscharntke et al. 2002a), but below a certain thresholds, sites become too small to hold viable populations. The size needed for viable populations differs between species (Shaffer 2007). Few accurate estimates exist for arthropods in calcareous grasslands, but habitat area has, for example, repeatedly been demonstrated to limit the occurrence of specialist grassland butterflies (Tscharntke et al. 2002a; Öckinger and Smith 2006). In chapter 7, I investigated the relationship between habitat area and species richness for carabid beetles, depending on their trophic level, habitat affinity and dispersal ability. Zoophagous, characteristic calcareous grassland species with poor dispersal ability proved most restricted to large habitat areas, being completely absent from sites smaller than 5 hectares. This group of species has been lost completely from the Dutch calcareous grasslands, where it was once represented e.g. by *Carabus convexus*. Also, zoophagous, characteristic calcareous grassland carabid beetles with better flight ability, e.g. *Brachinus crepitans*, are now restricted to the largest sites. Calcareous grassland size thus is a limiting factor, at least for part of the characteristic arthropod fauna in Dutch calcareous grasslands. This is not only worrying for arthropod conservation in general, but because trophic rank alters a species' vulnerability to habitat area, it also implies that trophic interactions may be seriously disrupted in sites smaller than 5 hectares (see chapter 7).

The area needed for viable populations increases with increasing environmental variability and increased occurrence of catastrophic events (Shaffer 2007). Habitat variability and the occurrence of catastrophic events can be expected to increase in calcareous grasslands due to climate change (Thomas et al. 2004; Opdam and Wascher 2004). Also the intensive management needed to compensate for the increased biomass productivity resulting from current high soil nutrient levels, can be viewed as such a catastrophic event for many arthropods. To increase resilience of arthropod populations to current and future global change, increasing the size of single sites, beyond the 5 hectare threshold, should thus receive top priority (see also Berendse et al. 2012).

Recent studies have demonstrated that nutrient-poor, species-rich vegetations can be recreated on fertilized agricultural land, if excess nutrients are removed and propagules are added, e.g. in the form of green hay (Mortimer et al. 1998; Kiehl et al. 2006; Kiehl and Wagner 2006; Woodcock et al. 2008; Smits 2010; Van Noordwijk et al. 2013). Such sites can form a valuable habitat for many calcareous grassland plant- and arthropod species (Kiehl and Wagner 2006; Woodcock et al. 2008; Smits 2010; Van Noordwijk et al. 2013, see also Box 3), although it has been questioned whether habitats closely resembling ancient calcareous grassland can be recreated within a short time-frame (Woodcock et al. 2008).

In general, development of arthropod communities shows a considerable time-lag compared to plant community development and arthropods with poor dispersal ability are particularly limited (Woodcock et al. 2008; Van Noordwijk et al. 2013). Targeted reintroduction, similar to green hay application for plants, is expected to dramatically improve restoration success for these species (Van Noordwijk and Klimkowska 2013).

The landscape context

Once species have been lost from a site, their chances of recolonization depend on the landscape context. The modeling study presented in chapter 6 indicated that in the current landscape, with 1% calcareous grassland, functional connectivity across the landscape is virtually non-existent, even for species with good dispersal ability. Field data generally support this conclusion, indicating that some dispersal over shorter distances occurs among good dispersers, but showing no indication of successful dispersal among poor dispersers or over longer distances. Among butterflies, reports of new populations of characteristic species have been largely restricted to the Sint Pietersberg, which is located close to a number of Belgian calcareous grassland sites (Post 2011). The ant data analysed in chapter 3 demonstrated that the presence of species with poor dispersal ability decreases exponentially with habitat isolation, with very few species present in sites that are more than 1 km removed from other calcareous grasslands. New colonizations by characteristic calcareous grassland arthropods on Verlengde Winkelberg were restricted to species with good dispersal ability (Van Noordwijk et al. 2013). Chapter 7 revealed that additional calcareous grassland had a positive effect on local species richness of carabid beetles, but this effect was restricted to a few hundred meters.

These results demonstrate that arthropod communities in most existing Dutch calcareous grasslands are not part of a meta-population structure, putting them at greater risk of local extinction (Hanski 1999). In addition, restoration of arthropod communities in restored sites is hampered by habitat isolation and targeted reintroduction measures will be needed to restore arthropod communities in these sites (Van Noordwijk et al. 2013). To improve long-term species persistence the amount of calcareous grassland in the landscape should be increased (see chapter 6). Efforts should focus on increasing calcareous grassland availability adjacent to, or within a few hundred metres of existing sites (chapter 6 and 7). Improving matrix quality, e.g. by increasing the quality of road verges seems not effective in increasing functional connectivity, especially for the most vulnerable species (chapter 6). Climate change is likely to increase the frequency of local population extinctions, which means that connected habitat patches in a meta-population structure will become even more important for long-term species persistence (see Box 3).

Integrating requirements of arthropods and plants

Conservation research has been strongly biased towards plants and vertebrate animals (Clark and May 2002). Invertebrate species only account for 11% of published conservation papers while they represent 79% of the species worldwide (Clark and May 2002). Also conservation policy and monitoring of restoration projects have been biased towards plants and vertebrate animals (Ruiz-Jaen and Aide 2005; Littlewood et al.

2012). It has long been suggested that if plant communities were restored, arthropods would automatically profit. This was fuelled by claims that plant species composition is a good predictor of arthropod species composition (Schaffers et al. 2008), even though it explained a mere 2-29% of the variance in arthropod species composition. Instead, evidence is mounting that restoration of plant communities does not ensure improvement of arthropod communities (e.g. Mortimer et al. 1998; Kruess and Tscharrntke 2002a; Öckinger et al. 2006; Woodcock et al. 2008; Konvicka et al. 2008). In fact, arthropod diversity is more sensitive than plant diversity, certainly when it comes to grazing management (chapter 4), but most likely also to habitat size (chapter 7) and global change in general (Thomas et al. 2004). Management strategies thus need to integrate the requirements of plants and arthropods to preserve arthropod biodiversity and the important ecosystem services provided by them (see chapter 1). This has often been viewed as a daunting task. Even among arthropods there are large differences in performance under conservation management (chapter 2; Oertli et al. 2005), potentially leading to conflicting management recommendations. The research in this thesis has uncovered a number of bottlenecks within calcareous grassland reserves for different taxonomic groups (i.e. lack of summer management for some ants and too intensive autumn grazing for butterflies). Previous studies on plants (Willems 2001; Smits 2010) found again other bottlenecks, especially insufficient nutrient removal. However, such different bottlenecks do not necessarily present a conflict when it comes to appropriate management strategies. The management recommendations given in this chapter for example, address all uncovered bottlenecks in an integrated way. Rotational grazing in spring and summer will create a warmer microclimate in summer and decreases disturbance of hibernating caterpillars. It is also expected to be more effective in removing excess nutrients (Bobbink and Willems 1991; Smits et al. 2009) and to provide valuable spatial variation in vegetation structure for phytophagous arthropods (Morris et al. 2005). Thus, while management strategies designed to benefit a single taxonomic group do not automatically benefit other taxa, integration of the various requirements of different taxonomic groups may often be achievable. Key to such integration of requirements into a single management regime is to understand the mechanisms underlying species responses to environmental stressors (both biotic and abiotic). This highlights the need for increased mechanistic understanding of how arthropods respond to their environment and increased attention for these requirements in conservation policy and management.

A Wasp spider (*Argiope bruennichi*) in a newly created calcareous grassland (Photo: Toos van Noordwijk)



References

- Abramoff, M.D., P.J. Magalhaes and S.J. Ram. 2004. Image processing with ImageJ. *Biophotonics International* 11:36–52.
- 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.
- Andelman, S.J. and W.F. Fagan. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *PNAS* 97:5954–5959.
- Andersen, A.N. 1995. A classification of Australian ant communities, based on functional-groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* 22:15–29.
- 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.
- Anderson, R., D. McFerran and A. Cameron. 2000. The ground beetles of Northern Ireland (Coleoptera-Carabidae). Ulster Museum Publication No. 279, Belfast.
- Andrasfalvy, A. 1961. Mitteilungen über Daten des Hochzeitsfluges verschiedener Ameisenarten in Ungarn und Ergebnisse von Versuchen der Koloniegründung im Formicar bei diesen Arten. *Insectes Sociaux* 8:299–310.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366.
- Archer, S., D.S. Schimel and E.A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change* 29:91–99.
- Arnold, J. 1983. Morphology, performance and fitness. *American Zoologist* 36:347–361.
- Aukema, B. 1983. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. Wantsen (Hemiptera, Heteroptera). *Natuurhistorisch Maandblad* 72:129–135.
- Aviron, S., F. Herzog, I. Klaus, B. Schüpbach and P. Jeanneret. 2010. Effects of wildflower strip quality, quantity, and connectivity on butterfly diversity in a Swiss arable landscape. *Restoration Ecology* 19:500–508.
- Baars, M.A., T.S. Van Dijk. 1984. Population dynamics of two carabid beetles at a Dutch heathland in relation to fluctuations, weather and dispersal. *Journal of Animal Ecology* 53:375–388.
- Baeten, L., D.I. Warton, H. Van Calster, P. De Frenne, G. Verstraeten, D. Bonte, M. Bernhardt-Römermann, J. Cornelis, G. Decocq, O. Eriksson, R. Hédli, T. Heinken, M. Hermy, P. Hommel, K. Kirby, T. Naaf, P. Petřík, G.-R. Walther, M. Wulf and K. Verheyen. 2014. A model-based approach to studying changes in compositional heterogeneity. *Methods in Ecology and Evolution* 5:156–164.
- Baguette, M. and H. Van Dyck. 2007. Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. *Landscape Ecology* 22:1117–1129.
- Baines, D., R.B. Sage and M.M. Baines. 1994. The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. *Journal of Applied Ecology* 31:776–783.
- Baiser, B., J.D. Olden, S. Record, J.L. Lockwood and M.L. McKinney. 2012. Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society B: Biological Sciences* 279:4772–4777.
- Bakker, E.S., H. Olf 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. Olf, 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. and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution* 14:63–68.
- 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.
- Baldock, D., G. Beaufoy, F. Brouwer and F. Godeschalk. 1996. Farming at the margins: abandonment or redeployment of agricultural land in Europe. IEE & IBN-DLO, London/The Hague.
- 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.
- Bardgett, R.D. and D.A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258–2268.
- Bartoń, K.A. 2013. MuMIn: Multi-model inference. R package version 1.9.11.
- Bartoń, K.A., B.L. Phillips, J.M. Morales and J.M.J. Travis. 2009. The evolution of an “intelligent” dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos* 118:309–319.
- Bartoń, K.A., T. Hovestadt, B.L. Phillips and J.M.J. Travis. 2012. Risky movement increases the rate of range expansion. *Proceedings of the Royal Society B: Biological Sciences* 279:1194–202.
- 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.
- Bascompte, J. and R.V. Sole. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology* 65:465–473.
- 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.
- Baum, K.A., K.J. Haynes, F.P. Dilleuth and J.T. Cronin. 2004. The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85:2671–2676.
- Bayfield, N. 1979. Some effects of trampling on *Molophilus-Ater* (Meigen) (Diptera, Tipulidae). *Biological Conservation* 16:219–232.
- Bell, J.R., C.P. Wheeler 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.
- 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* 46:69–114.
- 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.
- Berendse, F., B. van Leeuwen, B. Arts, T. Bade and S. Kuks. 2012. Onbeperkt houdbaar : advies voor een nieuw natuurbeleid in Nederland. *De Levende Natuur* 114:74–83.

- Berg, M.P. and H. Wijnhoven. 1997. Landpissebedden. Een tabel voor de landpissebedden (Crustacea; Oniscidae) van Nederland en België. KNNV Uitgeverij, Utrecht.
- Berg, M.P., E.T. Kiers, G. Driessen, M. van der Heijden, B.W. Kooi, F. Kuenen, M. Liefing, H.A. Verhoef and J. Ellers. 2010. Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16:587–598.
- 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.
- Beylich, A., H.-R. Oberholzer, S. Schrader, H. Hoepfer 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.
- Bink, F.A. 1992. Ecologische atlas van de dagvlinders van Noordwest-Europa. Schuyt & Co, Haarlem.
- Bischof, R., L.E. Loe, E.L. Meisinger, B. Zimmermann, B. Van Moorter and A. Myserud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *The American Naturalist* 180:407–24.
- Stork, N.E. and T.M. Blackburn. 1993. Abundance, body size and biomass of arthropods in tropical forest. *Oikos* 67:483–489.
- Blower, J.G. 1985. Millipedes. Synopsis of the British fauna. New series No. 35, Brill / Backhuys, Leiden.
- Bobbink, R. and J.P. Hettelingh. 2011. Review and revision of empirical critical loads and dose-response relationships. Proceedings of an expert workshop. Noordwijkerhout, 23–25 June 2010.
- Bobbink, R. and J.H. Willems. 1991. Impact of different cutting regimes on the performance of *Brachypodium pinnatum* in Dutch chalk grassland. *Biological Conservation* 56:1–21.
- Bobbink, R. and J.H. Willems. 1993. Restoration management of abandoned chalk grassland in the Netherlands. *Biodiversity and Conservation* 2:616–626.
- Bobbink, R. and J.H. Willems. 2001. OBN Preadvies Kalkgraslanden. Expertisecentrum LNV / Ministerie van LNV, Wageningen.
- Bobbink, R., M. Hornung and J.G.M. Roelofs. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86:717–738.
- Boer, P. 2010. Mieren van de Benelux. Stichting Jeugdbondsuitgeverij, 's-Graveland.
- Bokhorst, S., G.K. Phoenix, J.W. Bjerke, T.V. Callaghan, F. Huyer-Brugman and M.P. Berg. 2011. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Global Change Biology* 18:1152–1162.
- Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens and J.-S.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–35.
- Bonal, R. and A. Munoz. 2007. Multi-trophic effects of ungulate intraguild predation on acorn weevils. *Oecologia* 152:533–540.
- 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.

- Bonte, D., T. Hovestadt and H.J. Poethke. 2010. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos* 119:560–566.
- Bourke, A.F.G. and N.R. Franks. 1995. Social evolution in ants. Monographs in Behavior and Ecology. Princeton University Press, New York.
- Bourke, A.F.G. 1999. Colony size, social complexity and reproductive conflict in social insects. *Journal of Evolutionary Biology* 12:245–257.
- Bourn, N.A.D. and J.A. Thomas. 2002. The challenge of conserving grassland insects at the margins of their range in Europe. *Biological Conservation* 104:285–292.
- Bowler, D.E. and T.G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society* 80:205–25.
- Bradshaw, A.D. 1996. Underlying principles of restoration. *Canadian Journal of Fisheries and Aquatic Sciences* 53:3–9.
- Bremner, J., S.I. Rogers and C.L.J. Frid. 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators*. 6:609–622.
- Brooks, D.R., J.E. Bajer, S.J. Clark, D.T. Monteith, C. Andrews, S.J. Corbett, D.A. Beaumont and J.W. Chapman. 2012. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology* 49:1009–1019.
- Brown, J.H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124:255–279.
- Brown, V.K., C.W.D. Gibson, P.H. Sterling, S.H. Hillier, D.W.H. Walton and D.A. Wells. 1990. The mechanisms controlling insect diversity in calcareous grasslands. In: *Calcareous grasslands – ecology & management. Proceedings of a joint British Ecological Society/Nature Conservancy Council symposium* 79–87. University of Sheffield, 14–16 September 1987. Bluntisham Books, Huntingdon.
- Brown, J.H. and M.V. Lomolino. 2000. Concluding remarks: historical perspective and the future of island biogeography theory. *Global Ecology and Biogeography* 9:87–92.
- Calow, P. 1987. Towards a definition of functional ecology. *Functional Ecology* 1:57–61.
- Campbell, K. and M. Borner. 1995. Population trends and distribution of Serengeti herbivores: Implications for management. Pages 117–145 in: Sinclair, A.R.E. and P. Arcese (eds.). *Serengeti II dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago / London.
- Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation* 103:33–49.
- 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. and M.A. Leibold. 2003. Ecological niches: Linking classical and contemporary approaches 212. University of Chicago Press, Chicago/London.
- Cherrill, A.J. and V.K. Brown. 1992. Ontogenetic changes in the microhabitat preferences of *Decticus verrucivorus* (Orthoptera, Tettigoniidae) at the edge of its range. *Ecography* 15:37–44.
- Clark, J.A. and R.M. May. 2002. Taxonomic bias in conservation research. *Science* 297:191–192.
- Cobben, R.H. and G.J. Rozeboom. 1983. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. De Cicaden in bodemvallen (Hemiptera, Homoptera Auchenorrhyncha). *Natuurhistorisch Maandblad* 72:102–110.
- Collins, S.L. and S.C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64:87–94.

- Connor, E.F. and E.D. McCoy. 1979. The statistics and biology of the species-area relationship. *The American Naturalist* 113:791–833.
- Connor, E.F., A.C. Courtney, J.M. Yoder, S. Ecology and N. Mar. 2000. Individuals-area relationships : The relationship between animal population density and area. *Ecology* 81:734–748.
- Cristofoli, S., G. Mahy, R. Kekenbosch and K. Lambeets. 2010. Spider communities as evaluation tools for wet heathland restoration. *Ecological Indicators* 10:773–780.
- Cronin, J., 2004. Host-parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia* 139, 503–514.
- 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.
- Damuth, J. 1981. Population density and body size in mammals. *Nature* 290:699–700.
- Dauber, J., T. Purtauf, A. Allspach, J. Frisch, K. Voigtlander 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.
- Dauber, J., J. Bengtsson and L. Lenoir. 2006. Evaluating effects of habitat loss and land-use continuity on ant species richness in seminatural grassland remnants. *Conservation Biology* 20:1150–1160.
- Davies, K.F., C.R. Margules and J.F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81:1450–1461.
- Davies, K.F., C.R. Margules and J.F. Lawrence. 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* 85:265–271.
- De Boer, D. 1983. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. Mieren (Hymenoptera: Formicidae) – I. *Natuurhistorisch Maandblad* 72:5–12.
- De Vries, H.H., P.J. Den Boer and T.S. Van Dijk. 1996. Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia* 107:332–342.
- Dekoninck, W., H. De Koninck, J. Baugnée and J. Maelfait. 2007. Ant biodiversity conservation in Belgian calcareous grasslands: active management is vital. *Belgian Journal of Zoology* 137:137–146.
- Den Boer, P.J. 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia* 4:1–28.
- Den Boer, P.J. 1985. Fluctuations of density and survival of carabid populations. *Oecologia* 67:322–330.
- Den Boer, P.J. 1990a. Density limits and survival of local populations in 64 carabid species with different powers of dispersal. *Journal of Evolutionary Biology* 3:19–48.
- Den Boer, P. J. 1990b. The survival value of dispersal in terrestrial arthropods. *Biological Conservation* 54:175–192.
- Dennis, P. and M. Young. 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.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, 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.
- 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.

- 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., W. Dekoninck, D. Maes, M. Dufrêne, M. Jacobs, M. Pollet, E. Stassen and N. Thys. 2008. Een nieuwe verspreidingsatlas van de loopkevers en zandloopkevers (Carabidae) in België. Instituut voor Natuur- en Bosonderzoek & Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel.
- Devin S., J.-N. Beise, P. Usseglio-Polatera and J.-C. Moreteau. 2005. Changes in functional biodiversity in an invaded freshwater ecosystem: the Moselle River. *Hydrobiologia* 542:113–120.
- Dias N., M. Hassall and T. Waite. 2012. The influence of microclimate on foraging and sheltering behaviours of terrestrial isopods: Implications for soil carbon dynamics under climate change. *Pedobiologia* 55:137–144.
- Didham, R.K., J.H. Lawton, P.M. Hammond and P. Eggleton. 1998. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions: Biological Sciences* 353:437–451.
- Dieckmann, L. 1980. Beiträge zur Insektenfauna der DDR: Coleoptera: Curculionidae (Brachycerinae, Otiorhynchinae, Brachyderinae). *Beiträge zur Entomologie* 30:145–310.
- Diemont, W. and A. van de Ven. 1953. De kalkgraslanden van Zuid-Limburg. A. De Phanerogamen. *Publicaties van het Natuurhistorisch Genootschap Limburg* 6:3–20.
- Doerr, V.A.J., T. Barrett and E.D. Doerr. 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. *Journal of Applied Ecology* 48:143–147.
- Donath, T., N. Hölzel, A. Otte. 2003. The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Applied Vegetation Science* 6:13–22.
- 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* 168:660–81.
- Dormann, C.F., O. Schweiger, I. Augenstein, D. Bailey, R. Billeter, G. De Blust, R. DeFilippi, M. Frenzel, F. Hendrickx, F. Herzog, S. Klotz, J. Liira, J.-P. Maelfait, T. Schmidt, M. Speelmans, W.K.R.E. Van Wingerden and M. Zobel. 2007. Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography* 16:774–787.
- Dorp, D. and P.F.M. Opdam. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology* 1:59–73.
- Dover, J., S. Spencer, S. Collins, I. Hadjigeorgiou and A. Rescia. 2011. Grassland butterflies and low intensity farming in Europe. *Journal of Insect Conservation* 15:129–137.
- Doxa, A., M.L. Paracchini, P. Pointereau, V. Devictor and F. Jiguet. 2012. Preventing biotic homogenization of farmland bird communities: The role of High Nature Value farmland. *Agriculture Ecosystem and Environment* 148:83–88.
- Driscoll, D.A., S.C. Banks, P.S. Barton, D.B. Lindenmayer and A.L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution* 28:605–13.
- 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.
- Dufrêne, M. 1990. Etude préliminaire des taxocénoses de Carabides des pelouses calaminaires. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Entomologie* 126:141–150.

- 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.
- Ebeling, A., A.-M. Klein, W.W. Weisser and T. Tschardt. 2012. Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia* 169:453–465.
- Eckel, G. 1988. Vergleichende ökologische Untersuchungen an Laufkäfern auf Kalkmagerrasen und landwirtschaftlichen Nutzflächen der Kalkeifel (Carabidae, Coleoptera). Ph.D. thesis, Universität Bonn.
- EEA. 2004. High nature value farmland. Characteristics, trends and policy challenges. EEA Report No 1/2004, Copenhagen.
- Eidmann, H., 1943. Die Überwinterung der Ameisen. *Zoomorphology* 39:217–275.
- Ekroos, J., J. Heliölä and M. Kuussaari. 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology* 47:459–467.
- Ellis, S. 2003. Habitat quality and management for the Northern brown argus butterfly *Aricia artaxerxes* (Lepidoptera : Lycaenidae) in North East England. *Biological Conservation* 113:285–294.
- Englund, G. and P.A. Hambäck. 2007. Scale dependence of immigration rates: models, metrics and data. *Journal of Animal Ecology* 76:30–5.
- Everts, E. 1903 *Coleoptera Neerlandica, de schildvleugelige insecten van Nederland en het aangrenzend gebied. Deel 2.* Nijhoff, 's-Gravenhage.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- Fahrig, L. and G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* 66:1762–1768.
- FAO. 2008. Are grasslands under threat? Brief analysis of FAO statistical data on pasture and fodder crops.
- Farruggia, A., B. Dumont, A. Scohier, T. Leroy, P. Pradel and J.-P. Garel. 2012. An alternative rotational stocking management designed to favour butterflies in permanent grasslands. *Grass and Forage Science* 67:136–149.
- Fartmann, T. and G. Hermann. 2006 *Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa.* Landschaftsverband Westfalen-Lippe, Münster.
- 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.
- 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.
- 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.
- Franzén, M. and T. Ranius. 2004. Occurrence patterns of butterflies (Rhopalocera) in semi-natural pastures in southeastern Sweden. *Journal for Nature Conservation* 12:121–135.
- Freyman, 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.
- Gardner, R.H. and D.L. Urban. 2007. Neutral models for testing landscape hypotheses. *Landscape Ecology* 22:15–29.
- Gaston, K.J., T.M. Blackburn and J.H. Lawton. 1997. Interspecific abundance-range size relationships: an appraisal of mechanism. *Journal of Animal Ecology* 66:579–601.
- 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. Hamblen 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.
- Gish, M., A. Dafni and M. Inbar. 2011. Avoiding incidental predation by mammalian herbivores: accurate detection and efficient response in aphids. *Naturwissenschaften* 98:731–738.
- Goffart, P., M. Baguette, M. Dufrêne, L. Mousson, G. Nève, J. Sawchik, A. Wesierbs and P. Lebrun. 2001. Gestion des milieux semi-naturels et restauration de populations menacées de papillons de jour. Vol Travaux no. 25. Ministère de la Région Wallone, Direction générale des Ressources naturelles et de l'environnement, Division de la Nature et des Forêts, Jambes.
- Gomez, J.M. 2003. Herbivory reduces the strength of pollinator-mediated selection in the Mediterranean herb *Erysimum mediohispanicum*: Consequences for plant specialization. *The 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.
- Good, J.A. 2004. Calcareous grassland as a habitat for Staphylinidae (Coleoptera) in the Burren National Park, Co. Clare, Ireland. *Bulletin of the Irish Biogeographical Society* 28:147–162.
- Goulet, H. 2003. Biodiversity of ground beetles (Coleoptera: Carabidae) in Canadian agricultural soils. *Canadian Journal of Soil Science* 83:259–264.
- Green, R.E., S.J. Cornell, J.P.W. Scharlemann and A. Balmford. 2005. Farming and the fate of wild nature. *Science* 307:550–555.
- Greenhouse, S.W. and S. Geisser. 1959. On methods in the analysis of profile data. *Psychometrika* 24:95–112.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- Gruner, H.-E. 1966. Krebstiere oder Crustacea V. Isopoda. 2. Lieferung. Die Tierwelt Deutschlands und der angrenzenden Meeresteile 53. Gustav Fischer Verlag, Jena.
- Gutierrez, D. and R. Menendez. 1997. Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Caraboidea) in relation to dispersal ability. *Journal of Biogeography* 24:903–914.
- Gutiérrez, D., C.D. Thomas and J.L. León-Cortés. 1999. Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). *Oecologia* 121:506–517.
- 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.
- 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.

- Haila, Y. 2002. A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecological Applications* 12:321–334.
- Hannig, K., H. Terlutter and J. Lückmann. 2005. Die Laufkäferfauna (Col., Carabidae) ausgewählter Kalkmagerrasen des oberen Diemeltales. *Natur und Heimat* 65:113–122.
- Hanski, I. 1999. *Metapopulation Ecology*. Oxford series in Ecology and Evolution. Oxford University Press.
- Hanski, I., G.A. Zurita, M.I. Bellocq and J. Rybicki. 2013. Species-fragmented area relationship. *PNAS* 110:12715–20.
- Hastings, A. 1980. Disturbance, coexistence, history and competition for space. *Theoretical Population Biology* 18:363–373.
- Hedges, L.V., J. Gurevitch and P.S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156.
- Heijerman, T. and K. Booij. 1983. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. Bodembewonende snuitkevers (Coleoptera: Curculionidae). *Natuurhistorisch Maandblad* 72:164–172.
- Heino, J. 2008. Temporally stable abundance-occupancy relationships and occupancy frequency patterns in stream insects. *Oecologia* 157:337–47.
- Heller, N.E. and E.S. Zavaleta. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation* 142:14–32.
- Hengeveld, R. 1985. Dynamics of Dutch beetle species during the twentieth century (Coleoptera, Carabidae). *Journal of Biogeography* 12:389–411.
- Henle, K., K.F. Davies, M. Kleyer, C. Margules and J. Settele. 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* 13:207–251.
- Hillegers, H. 1984. De geschiedenis van de vegetatie en de functionele betekenis van de Bemelerberg. *Publicaties van het Natuurhistorisch Genootschap in Limburg* 34:13–18.
- Hillegers, H. P. M. 1993. Heerdgang in Zuidelijk Limburg: een vorm van extensieve beweiding in verleden, heden en toekomst. *Publicaties van het Natuurhistorisch Genootschap in Limburg*, No 40.
- 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: Danell, K., R. Bergstrom, P. Duncan and J. Pastor (eds.). *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge University Press, Cambridge.
- Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology* 6:324–337.
- Hobbs, R. and D. Norton. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4:93–110.
- Hobbs, N.T. and D.M. Swift. 1988. Grazing in herds – when are nutritional benefits realized? *The American Naturalist* 131:760–764.
- Hodgson, J.G., J.P. Grime, P.J. Wilson, K. Thompson and S.R. Band. 2005. The impacts of agricultural change (1963–2003) on the grassland flora of Central England: processes and prospects. *Basic and Applied Ecology* 6:107–118.
- Hodgson, J.A., C.D. Thomas, B.A. Wintle and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology* 46:964–969.
- Hodgson, J.A., A. Moilanen, B.A. Wintle and C.D. Thomas. 2011a. Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology* 48:148–152.

- Hodgson, J.A., C.D. Thomas, S. Cinderby, H. Cambridge, P. Evans and J. K. Hill. 2011b. Habitat re-creation strategies for promoting adaptation of species to climate change. *Conservation Letters* 4:289–297.
- Hodgson, J.A., C.D. Thomas, C.Dytham, J.M.J. Travis and S.J. Cornell. 2012. The speed of range shifts in fragmented landscapes. *PloS one* 7:e47141.
- Hofmann, T.A.A. and C.F.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.
- Højsgaard, S., U. Halekoh and J. Yan. 2006. The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software* 15:1–11.
- Hölldobler, B. and E.O. Wilson. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.
- Holt, R.D., J.H. Lawton, G.A. Polis and N.D. Martinez. 1999. Trophic rank and the species-area relationship. *Ecology* 80:1495–1504.
- Humbert, J.-Y., J. Ghazoul and T. Walter. 2009. Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems & Environment* 130:1–8.
- Humbert, J.-Y., J. Ghazoul, N. Richner and T. Walter. 2010. Hay harvesting causes high orthopteran mortality. *Agriculture, Ecosystems & Environment* 139:522–527.
- Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *The American Naturalist* 93:145–159.
- 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.
- Huxel, G.R. and A. Hastings. 1999. Habitat loss, fragmentation, and restoration. *Restoration Ecology* 7:309–315.
- IPCC. 2007. *Climate Change 2007: Synthesis report*. Contribution of working groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate Change.
- Isard, S. and S. Gage. 2001. *Flow of life in the atmosphere: an airscape approach to invasive organisms*. Michigan State University Press.
- 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.
- 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.
- Joern, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86:861–873.
- Joern, A. and A.N. Laws. 2013. Ecological mechanisms underlying arthropod diversity in grasslands. *Annual Reviews of Entomology* 58:19–36.
- Joern, A. and L.R. Lawlor. 1981. Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos* 37:93–104.
- Johnson, R.A. 2006. Capital and income breeding and the evolution of colony founding strategies in ants. *Insectes Sociaux* 53:316–322.

- Jongejans, E., O. Skarpaas and K. Shea. 2008. Dispersal, demography and spatial population models for conservation and control management. *Perspectives in Plant Ecology, Evolution and Systematics* 9:153–170.
- Kahmen, S., P. Poschlod and K.F. Schreiber. 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation* 104:319–328.
- Kaplan, I. and R.F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters* 10:977–994.
- Keddy, P.A. 1992. A pragmatic approach to functional ecology. *Functional Ecology* 6:621–626.
- 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.
- Keller, L. and L. Passera. 1989. Size and fat-content of gynes in relation to the mode of colony founding in ants (Hymenoptera, Formicidae). *Oecologia* 80:236–240.
- Kerr, J.T. and J. Cihlar. 2004. Patterns and causes of species endangerment in Canada. *Ecological Applications* 14:743–753.
- Keymer, J.E., P.A. Marquet, J.X. Velasco-Hernández and S.A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *The American Naturalist* 156:478–494.
- Kiehl, K. and C. Wagner. 2006. Effect of hay transfer on long-term establishment of vegetation and grasshoppers on former arable fields. *Restoration Ecology* 14:157–166.
- Kiehl, K., A. Thormann and J. Pfadenhauer. 2006. Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. *Restoration Ecology* 14:148–156.
- King, A.W. and K.A. With. 2002. Dispersal success on spatially structured landscapes: When do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147:23–39.
- Kipyatkov, V.E. 1993. Annual cycles of development in ants: diversity, evolution, regulation. *Proceedings of the Colloquia on Social Insects* 2:25–48.
- Kipyatkov, V.E. 2001. Seasonal life-cycles and the forms of dormancy in ants (Hymenoptera, Formicoidea). *Acta Societas Zoologicae Bohemicae* 65:198–217.
- Kipyatkov, V.E., E.B. Lopatina, A.A. Imamgaliev and L.A. Shirokova. 2004. Effect of temperature on rearing of the first brood by the founder females of the ant *Lasius niger* (Hymenoptera, Formicidae): Latitude-dependent variability of the response norm. *Journal of Evolutionary Biochemistry and Physiology* 40:165–175.
- Kleukers, R.M.J.C., E. J. van Nieukerken, B. Odé, L.P.M. Willemse and W.K.R.E. van Wingerden. 1997. De sprinkhanen en Nederland, krekels van (Orthoptera). *Nederlandse Fauna* 1. Nationaal Natuurhistorisch Museum Naturalis / European Invertebrate Survey, Leiden.
- Kleyer, M., R.M. Bekker, I.C. Knevel, J.P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J.M. Van Groenendaal, L. Klimeš, J. Klimešová, S. Klotz, G.M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J.G. Hodgson, A.-K. Jackel, I. Kühn, D. Kunzmann, W.A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H.J. Steendam, O. Tackenberg, B. Wilmann, J.H.C. Cornelissen, O. Eriksson, E. Garnier and B. Peco. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96:1266–1274.
- Knol, R. and J. H. J. Schaminée. 2004. De Zuid-Limburgse kalkgraslanden in Europees perspectief. *Stratiotes* 28/29:53–62.
- Konvicka, M., J. Benes, O. Cizek, F. Kopecek, O. Konvicka and L. Vitaz. 2008. How too much care kills species: Grassland reserves, agri-environmental schemes and extinction of *Colias myrmidone* (Lepidoptera: Pieridae) from its former stronghold. *Journal of Insect Conservation* 12:519–525.
- Koomen, P. 1986. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. Spinnen (Arachnida, Araneae) van het Gerendal en de Kruisberg. *Natuurhistorisch Maandblad* 75:198–207.

- Kotiaho, J.S., V. Kaitala, A. Komonen and J. Paovinen. 2004. Predicting the risk of extinction from shared ecological characteristics. *PNAS* 102:1963–1967.
- Krauss, J., R. Bommarco, M. Guardiola, R.K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Ockinger, M. Pärtel, J. Pino, J. Pöyry, K.M. Raatikainen, A. Sang, C. Stefanescu, T. Teder, M. Zobel and I. Steffan-Dewenter. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters* 13:597–605.
- 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.
- Kuussaari, M. 1998. Biology of the Glanville fritillary butterfly (*Melitaea cinxia*). Ph.D. thesis, Helsinki University.
- Laiolo, P., F. Dondero, E. Ciliento and A. Rolando. 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine fauna. *Journal of Applied Ecology* 41:294–304.
- Lambeets, K., M.L. Vandegehuchte, J.-P. Maelfait and D. Bonte. 2008. Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology* 77:1162–1174.
- Lambeets, K., M.L. Vandegehuchte, J.P. Maelfait and D. Bonte. 2009. Integrating environmental conditions and functional life-history traits for riparian arthropod conservation planning. *Biological Conservation* 142:625–637.
- 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.
- Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* 28:23–39.
- 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.
- Lawton, J.H. and M.P. Hassell. 1981. Asymmetrical competition in insects. *Nature* 289:793–795.
- Lenoir, L. and T. Lennartsson. 2010. Effects of timing of grazing on arthropod communities in semi-natural grasslands. *Journal of Insect Science* 10:1–24.
- Lezama, F., S. Baeza, A. Altesor, A. Cesa, E. J. Chaneton and J. M. Paruelo. 2013. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science* 15:8–21.
- Liddle, M. 1997. Recreation ecology: The ecological impact of outdoor recreation and ecotourism. Chapman & Hall, London.
- Lindroth, C.H. 1949. Die Fennoskandischen Carabidae Teil III. Elanders, Stockholm.
- 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. 2012. Science into practice – how can fundamental science contribute to better management of grasslands for invertebrates? *Insect Conservation and Diversity* 5:1–8.
- Lockwood, J.L., M. Hoopes and M. Marchetti. 2007. *Invasion Ecology*. Blackwell Publishing.

- 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, 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.
- 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.
- Mabelis, A.A., 1983. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. Mieren (Hymenoptera: Formicidae) – II. *Natuurhistorisch Maandblad* 72:33–37.
- Mabelis, A.A., 1994. Flying as a survival strategy for wood ants in a fragmented landscape (Hymenoptera, Formicidae). *Memorabilia Zoologica* 48:147–170.
- Mabelis, A.A. and J.P. Chardon. 2006. Survival of the Trunk ant (*Formica truncorum* Fabricius, 1804; Hymenoptera: Formicidae) in a fragmented habitat. *Myrmecological News* 9:1–11.
- Mabelis, A.A. and J. Korczyńska. 2001. Dispersal for survival : some observations on the trunk ant (*Formica truncorum* Fabricius). *Netherlands Journal of Zoology* 51:299–321.
- Mabelis, A.A. and B. Verboom. 2009. Ongewervelde dieren van versnipperde schrale graslanden van Zuid-Limburg. *Natuurhistorisch Maandblad* 98:189–201.
- MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, New York.
- 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 decomposition of dung pats. *Journal of Applied Ecology* 27:1–15.
- Maes, D., A. Ghesquiere, M. Logie and D. Bonte. 2006. Habitat use and mobility of two threatened coastal dune insects: Implications for conservation. *Journal of Insect Conservation* 10:105–115.
- Mattila, N., V. Kaitala, A. Komonen, J.S. Kotiaho and J. Päävinen. 2006. Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology* 20:1161–1168.
- 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: Sinclair, A.R.E. and P. Arcese (eds.). *Serengeti II dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago / London.
- 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.
- McGill, B.J., B.J. Enquist, E. Weiher and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:178–185.
- McKinney, M. and J. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14:450–453.
- McKinney, M.L. and J.L. Lockwood. 2001. Biotic homogenization: A sequential and selective process. Pages 1–17 in: Lockwood, J.L. and M.L. McKinney (eds.). *Biotic homogenization*. Springer US, Boston, MA.
- McLean, I.F.G., S.H. Hillier, D.W.H. Walton and D.A. Wells. 1990. The fauna of calcareous grasslands. Pages 41–46 in: Hillier, S.H.H., D.W.H. Walton and D.A. Wells (eds.). *Calcareous grasslands: ecology & management*. Bluntisham Books, Huntingdon.

- McNaughton, S.J. 1976. Serengeti migratory Wildebeest: facilitation of energy flow by grazing. *Science* 191:92–94.
- McNaughton, S.J. 1984. Grazing lawns – Animals in herds, plant form, and coevolution. *The American Naturalist* 124:863–886.
- McNaughton, S.J. 1986. On plants and herbivores. *The American Naturalist* 128:765–770.
- Melis, C., I. Teurlings, J.C. Linnell, R. Andersen and A. Bordonì. 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.
- Merckx, T. and H. Van Dyck. 2007. Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, *Pararge aegeria* L. *Animal Behaviour* 74:1029–1037.
- Michener, W.K. 1997. Quantitatively evaluating restoration experiments: Research design, statistical analysis, and data management considerations. *Restoration Ecology* 5:324–337.
- 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.
- 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.
- Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: Biodiversity synthesis. Washington, DC.
- 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: Duffey, E. and A.S. Watt (eds.). *The scientific management of animal and plant communities for conservation*. Blackwell scientific publications, Oxford / London / Edinburgh.
- Morris, M.G. 1973. The effects of seasonal grazing on the heteroptera and auchenorhyncha (Hemiptera) of chalk grassland. *Journal of Applied Ecology* 10:761–780.
- Morris, M.G. 1979. Responses of grassland invertebrates to management by cutting. II. Heteroptera. *Journal of Applied Ecology* 16:417–432.
- Morris, M.G. 1997. Broad-nosed weevils. Coleoptera: Curculionidae (Entiminae). *Handbooks for the identification of British insects* 5, 17a:1–106.
- 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. 2002. True weevils (Part I) Coleoptera: Curculionidae (subfamilies Raymondionyminae to Smicronychinae). *Handbooks for the identification of British insects* 5, 17b:1–149.
- Morris, M.G. and W.E. Rispin. 1988. A beetle fauna of oolitic limestone grassland, and the responses of species to conservation management by different cutting regimes. *Biological Conservation* 43:87–105.
- 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 Auchenorhyncha. *Journal of Insect Conservation* 9:363–374.
- Morris, M.G., S.H. Hillier, D.W.H. Walton and D.A. Wells. 1990. The effects of management on the invertebrate community of calcareous grasslands. Pages 128–133 in: Hillier, S.H.H., D.W.H. Walton and D.A. Wells (eds.). *Calcareous grasslands: ecology & management*. Bluntisham Books, Huntingdon.
- Mortimer, S.R., J.A. Hollier and V.K. Brown. 1998. Interactions between plant and insect diversity in the restoration of lowland calcareous grasslands in southern Britain. *Applied Vegetation Science* 1:101–114.

- Mortimer, S.R., R.G. Booth, S.J. Harris and V.K. Brown. 2002. Effects of initial site management on the Coleoptera assemblages colonising newly established chalk grassland on ex-arable land. *Biological Conservation* 104:301–313.
- Mouillot, D., D.R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, L. Lavergne S. Lavorel, N. Mouquet, C.E.T. Paine, J. Renaud and T. Thuiller. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol* 11:e1001569.
- Murdoch, W.W., C.H. Peterson and F.C. Evans. 1972. Diversity and pattern in plants and insects. *Ecology* 53:819–829.
- 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.
- Nathan, R., W.M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz and P.E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *PNAS* 105:19052–19059.
- Negro, M., A. Rolando and C. Palestini. 2011. The impact of overgrazing on dung beetle diversity in the Italian Maritime Alps. *Environmental Entomology* 40:1081–1092.
- Negro, M., C. La Rocca, S. Ronzani, A. Rolando and C. Palestini. 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.
- Neubert, M. G. and H. Caswell. 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81:1613–1628.
- 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.
- 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.
- Oates, M.R. 1995. Butterfly conservation within the management of grassland habitats. Pages 98–112 in: Pullin, A.S. (ed.). *Ecology and conservation of butterflies*. Chapman and Hall, London.
- Öckinger, E. and H.G. Smith. 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia* 149:526–34.
- 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.
- Öckinger, E., O. Schweiger, T.O. Crist, D.M. Debinski, J. Krauss, M. Kuussaari, J.D. Petersen, J. Pöyry, J. Settele, K.S. Summerville and R. Bommarco. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters* 13:969–979.
- 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., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O’Hara, G.L. Simpson, P. Solymos, M.H. H. Stevens and H. Wagner. 2013. *Vegan: Community ecology package*. R package, version 2.0-7.
- Olden, J.D., N. Leroy Poff, M.R. Douglas and K.D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution* 19:18–24.
- Olf, 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* 415:901–904.
- 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.
- Onsager, J.A. 2000. Suppression of grasshoppers in the Great Plains through grazing management. *Journal of Range Management* 53:592–602.
- Opdam, P. and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 117:285–297.
- Ostermann, O.P. 1998. The need for management of nature conservation sites designated under Natura 2000. *Journal of Applied Ecology* 35:968–973.
- Östman, Ö. 2005. Asynchronous temporal variation among sites in condition of two carabid species. *Ecological Entomology* 30:63–69.
- Owensmith, N. 1989. Megafaunal Extinctions – the conservation message from 11,000 Years BP. *Conservation Biology* 3:405–412.
- Ozinga, W.A., J.H.J. Schaminée, R.M. Bekker, S. Bonn, P. Poschlod, O. Tackenberg, J. Bakker and J.M. van Groenendael. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108:555–561.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Parsons, A.J. and B. Dumont. 2003. Spatial heterogeneity and grazing processes. *Animal Research* 52:161–179.
- Pe’er, G. and S. Kramer-Schadt. 2008. Incorporating the perceptual range of animals into connectivity models. *Ecological Modelling* 213:73–85.
- Pe’er, G., K. Henle, C. Dislich and K. Frank. 2011. Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. *PloS one* 6:e22355.
- Peet, R.K., D.C. Glenn-Lewin and J.W. Walker-Wolf. 1983. Prediction of man’s impact on plant species diversity. Pages 41–54 in: Holzner, W., M.J.A. Werger and I. Ikusima (eds.). *Man’s impact on vegetation*. Junk Publishers, The Hague, The Netherlands.
- 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.
- 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.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391–409.
- Polis, G.A., C.A. Myers and R.D. Holt. 1989. The ecology and evolution of intraguild predation – potential competitors that eat each other. *Annual Review of Ecology, Evolution, and Systematics* 20:297–330.
- Polus, E., S. Vandewoestijne, J. Choutt and M. Baguette. 2007. Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. *Biodiversity and conservation* 16:3423–3436.
- Poschlod, P. and M.F. WallisDeVries. 2002. The historical and socioeconomic perspective of calcareous grasslands – lessons from the distant and recent past. *Biological Conservation* 104:361–376.
- Post, F. 2011. Vlinders op de Sint-Pietersberg. Ter Haar, Snellen.

- Potts, S.G., B.A. Woodcock, S.P.M. Roberts, T. Tscheulin, E.S. Pilgrim, V.K. Brown and J.R. Tallwin. 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.
- Prache, S., I.J. Gordon, A.J. Rook. 1998. Foraging behaviour and diet selection in domestic herbivores. *Annales De Zootechnie* 47:335–345.
- 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.S. Newbold, S. Parsons and A. Joern. 2013. Invertebrates, ecosystem services and climate change. *Biological reviews of the Cambridge Philosophical Society* 88:327–48.
- Preston, F.W. 1960. Time and space and the variation of species. *Ecology* 41:612–627.
- Prevedello, J.A. and M.V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* 19:1205–1223.
- 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.
- Purtauf, T., J. Dauber and V. Wolters. 2005. The response of carabids to landscape simplification differs between trophic groups. *Oecologia* 142:458–64.
- Pywell, R.F., W.R. Meek, L. Hulmes, S. Hulmes K.L. James, M. Nowakowski and C. Carvell. 2011. Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. *Journal of Insect Conservation* 15:853–864.
- R Development Core Team. 2013. R: A language and environment for statistical computing. version 3.0.1. R Foundation for Statistical Computing, Vienna, Austria; www.R-project.org.
- Reitz, S.R. and J.T. Trumble. 2002. Competitive displacement among insects and arachnids. *Annual Review of Entomology* 47:435–65.
- Rheinheimer, J. and M. Hassler. 2010. Die Rüsselkäfer Baden-Württembergs. *Naturschutz-Spektrum. Themen* 99. Verlag Regionalkultur.
- Ribera, I., G.N. Foster, I.S. Downie, D.I. McCracken and V.J. Abernethy. 1999. A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). *Annales Zoologici Fennici* 36:21–37.
- Ribera, I., S. Dolédec, I.S. Downie and G.N. Foster. 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* 82:1112–1129.
- 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.
- Ritchie, M.E. 2000. Nitrogen limitation and trophic vs. abiotic influence on insect herbivores in a temperate grassland. *Ecology* 81:1601–1612.
- Roguet, C., B. Dumont and S. Prache. 1998. Selection and use of feeding sites and feeding stations by herbivores: A review. *Animal Research* 47:225–244.
- Römermann, C., O. Tackenberg, A.-K. Jackel and P. Poschlod. 2008. Eutrophication and fragmentation are related to species' rate of decline but not to species rarity: results from a functional approach. *Biodiversity and conservation* 17:591–604.

- Rothenwöhrer, C., C. Scherber and T. Tschardtke. 2013. Grassland management for stem-boring insects: Abandoning small patches is better than reducing overall intensity. *Agriculture, Ecosystems & Environment* 167:38–42.
- 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.
- Ruiz-Jaen, M.C. and M.T. Aide. 2005. Restoration success: How is it being measured? *Restoration Ecology* 13:569–577.
- 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.
- Sala, O.E. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Samways, M.J. 1994. *Insect conservation biology*. Chapman and Hall, London.
- 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.
- Saska, P. 2004. Carabid larvae as predators of weed seeds: granivory in larvae of *Amara eurynota* (Coleoptera: Carabidae). *Communications in Agricultural and Applied Biological Sciences* 69:27–33.
- Saska, P. 2005. Contrary food requirements of the larvae of two *Curtonotus* (Coleoptera: Carabidae: *Amara*) species. *Annals of Applied Biology* 147:139–144.
- Schaffers, A.P., I. Raemakers, K.V. Sykora and C.J.F. Ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89:782–794.
- Schaminée, J.H.J., S.M. Hennekens and W.A. Ozinga. 2012. The Dutch national vegetation database. *Biodiversity & Ecology* 4:201–209.
- 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. Tschardtke. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468:553–6.
- Scherf, H. 1964. Die Entwicklungsstadien der mitteleuropäischen Curculioniden (Morphologie, Bionomie, Ökologie). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 506:1–335.
- Schlick-Steiner, B.C., F.M. Steiner, K. Moder, A. Bruckner, K. Fiedler and E. Christian. 2006. Assessing ant assemblages: pitfall trapping versus nest counting (Hymenoptera, Formicidae). *Insectes Sociaux* 53:274–281.
- Schmitz, O.J. 2011. *Resolving ecosystem complexity. Monographs in Population Biology* 47:176. Princeton University Press, Princeton.
- Schoeters, E. and F. Vankerkhoven. 2001. *Onze mieren. Educatie Limburgs Landschap vzw, Heusden-Zolder*.
- Scholl, P.J. 1993. Biology and control of cattle grubs. *Annual Review of Entomology* 38:53–70.

- Schtickzelle, N. and G. Mennechez. 2006. Dispersal depression with habitat fragmentation in the Bog fritillary butterfly. *Ecology* 87:1057–1065.
- Schtickzelle, N., C. Turlure and M. Baguette. 2007a. Grazing management impacts on the viability of the threatened Bog fritillary butterfly *Proclossiana eunomia*. *Biological Conservation* 136:651–660.
- Schtickzelle, N., A. Joiris, H. Van Dyck and M. Baguette. 2007b. Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* 7:4.
- Seastedt, T.R. and D.A. Crossley. 1984. The influence of arthropods on ecosystems. *Bioscience* 34:157–161.
- Seifert, B. 1996. Ameisen: beobachten, bestimmen. Naturbuch Verlag, Augsburg.
- Seifert, B. 2007. Die Ameisen Mittel- und Nordeuropas. Lutra Verlags- und Vertriebsgesellschaft, Goerlitz / Tauer.
- Shaffer, M.L. 2007. 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.
- Shaw, J.D., D. Spear, M. Greve and S.L. Chown. 2010. Taxonomic homogenization and differentiation across Southern Ocean Islands differ among insects and vascular plants. *Journal of Biogeography* 37:217–228.
- Shepherd, U.L. and S.L. Brantley. 2005. Expanding on Watson's framework for classifying patches: when is an island not an island? *Journal of Biogeography* 32:951–960.
- Shipley, B. 2004. Cause and correlation in biology a user's guide to path analysis, structural equations and causal inference. Cambridge University Press.
- Siegfried, W.R. 1990. Tail length and biting insects of ungulates. *Journal of Mammalogy* 71:75–78.
- Siemann, E., D. Tilman, J. Haarstad and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist* 152:738–750.
- Siepel, H. 1994. Life-history tactics of soil microarthropods. *Biology and Fertility of Soils* 18:263–278.
- Siepel, H. 1995. Applications of microarthropod life-history tactics in nature management and ecotoxicology. *Biology and Fertility of Soils* 19:75–83.
- Smee, M. W. Smyth, M. Tunmore, R. French-Constant and D. Hodgson. 2011. Butterflies on the brink: habitat requirements for declining populations of the marsh fritillary (*Euphydryas aurinia*) in SW England. *Journal of Insect Conservation* 15:153–163.
- Smith, C.C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. *Ecology* 21:381–397.
- Smits, N.A.C. 2010. Restoration of nutrient-poor grasslands in Southern Limburg. Ph.D. thesis, Utrecht University.
- Smits, N.A.C., C.G.E. van Noordwijk, R. Bobbink, H. Esselink, H.P.J. Huiskes, L. Kuiters, W. Ozinga, J.H.J. Schaminee, H. Siepel, W.C.E.P. Verberk and J.H. Willems. 2009. Onderzoek naar de ecologische achteruitgang en het herstel van Zuid-Limburgse hellingschraallandcomplexen. Ministerie van LNV, Directie Kennis, Ede.
- Sommer, K. and B. Hölldobler. 1995. Colony founding by queen association and determinants of reduction in queen number in the ant *Lasius niger*. *Animal Behaviour* 50:287–294.
- Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46:336–365.
- Spiesman, B.J. and B.D. Inouye. 2013. Habitat loss alters the architecture of plant – pollinator interaction networks. *Ecology* 94:2688–2696.

- Stearns, S.C. 1976. Life-history tactics: A review of the ideas. *The Quarterly Review of Biology* 51:3–47.
- Steffan-Dewenter, I. and T. Tschardtke. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121:432–440.
- Steffan-Dewenter, I. and T. Tschardtke. 2000. Butterfly community structure in fragmented habitats. *Ecology Letters* 3:449.
- Steffan-Dewenter, I. and T. Tschardtke. 2002. Insect communities and biotic interactions on fragmented calcareous grasslands – a mini review. *Biological Conservation* 104:275–284.
- Stevens, C.J., N.B. Dise, J.O. Mountford and D.J. Gowing. 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303:1876–9.
- Stille, M. 1996. Queen/worker thorax volume ratios and nest-founding strategies in ants. *Oecologia* 105:87–93.
- Stitz, H. 1939. *Hautflügler oder Hymenoptera I: Ameisen oder Formicidae*. Gustav Fischer Verlag, Jena.
- Stoutjesdijk, P. and J.J. Barkman. 1992. Microclimate, vegetation and fauna. Opulus Press AB, Knivsta.
- Strong, D.R., J.H. Lawton and T.R.E. Southwood. 1984. *Insects on plants. Community patterns and mechanisms*. Blackwell Scientific publications, Oxford.
- Suominen, O. and K. Danell. 2006. Effects of large herbivores on other fauna. Pages 383–412 in: Danell, K., R. Bergstrom, P. Duncan and J. Pastor (eds.). *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge University Press, Cambridge.
- Swihart, R.K., T.M. Gehring and M.B. Kolozsvary. 2003. Responses of “resistant” vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Diversity and Distributions* 9:1–18.
- Taylor, P.D. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571–573.
- Thiele, H.U. 1977. *Carabid beetles in their environments: A study on habitat selection by adaptations in physiology and behaviour*. Springer-Verlag, Berlin / Heidelberg / New York.
- Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M.F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. Van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips and S.E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145–8.
- 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.
- Thomas, J.A., D.J. Simcox and T. Hovestadt. 2011. Evidence based conservation of butterflies. *Journal of Insect Conservation* 15:241–258.
- Tilman, D. 1986. A consumer-resource approach to community structure. *American Zoologist* 26:5–22.
- Tilman, D., R.M. May, L. Lehman and M.A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* 371:65–66.
- Travis, J.M.J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B: Biological Sciences* 270:467–73.
- Travis, J.M.J., K. Mustin, K.A. Bartoń, T.G. Benton, J. Clobert, M.M. Delgado, C. Dytham, T. Hovestadt, S.C.F. Palmer, H. Van Dyck and D. Bonte. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution* 3:628–641.

- Travis, J.M.J., M. Delgado, G. Bocedi, M. Baguette, K. Barton, D. Bonte, I. Boulangeat, J.A. Hodgson, A. Kubisch, V. Penteriani, M. Saastamoinen, V.M. Stevens and J.M. Bullock. 2013. Dispersal and species' responses to climate change. *Oikos* 122:1532–1540.
- 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: Gange, K. and V. K. Brown (eds.). *Multitrophic interactions in terrestrial ecosystems*. Blackwell Science, Oxford.
- Tscharntke, T. and A. Kruess. 1999. Habitat fragmentation and biological control. Pages 190–205 in: Hawkins, B.A. and H.V. Cornell (eds.). *Theoretical approaches to biological control*. Cambridge University Press, Cambridge.
- Tscharntke, T., I. Steffan-Dewenter, A. Kruess and C. Thies. 2002a. Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research* 17:229–239.
- Tscharntke, T., I. Steffan-Dewenter, A. Kruess and C. Thies. 2002b. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications* 12:354–363.
- Tscharntke, T., T.A. Rand and F.J.J.A. Bianchi. 2005. The landscape context of trophic interactions: insect spillover across the crop – noncrop interface. *Annales Zoologici Fennici* 42:421–432.
- 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. Fründ, 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 of the Cambridge Philosophical Society* 87:661–85.
- Tschinkel, W.R., 1991. Insect sociometry, a field in search of data. *Insectes Sociaux* 38:77–82.
- Turin, H. 1983. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. Loopkevers (Coleoptera Carabidae) van kalkgraslanden en hellingbossen. *Natuurhistorisch Maandblad* 72:73–83.
- Turin, H. 2000. De Nederlandse loopkevers: Verspreiding en oecologie (Coleoptera: Carabidae). *Nederlandse Fauna deel 3*. Nationaal Natuurhistorisch Museum Naturalis / European Invertebrate Survey, KNNV Uitgeverij, Leiden.
- Van der Made, J.G. 1983. Dagvlinders, wegwijzers voor een geïntegreerd beheer van kalkgraslanden? *Publicaties van het Natuurhistorisch Genootschap van Limburg* 33:13–17.
- Van Dyck, H. 2012. Changing organisms in rapidly changing anthropogenic landscapes: the significance of the “Umwelt”-concept and functional habitat for animal conservation. *Evolutionary Applications* 5:144–153.
- Van Dyck, H. and M. Baguette. 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology* 6:535–545.
- Van Etten, J. and M. Roos. 1984. De invertebratenfauna van de Zuidlimburgse kalkgraslanden. Landpissebedden (Crustacea: Isopoda: Oniscoidea). *Natuurhistorisch Maandblad* 73:5–12.
- Van Kleef, H.H., W.C.E.P. Verberk, R.S.E.W. Leuven, H. Esselink, G. Van Der Velde and G.A. Van Duinen. 2006. Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. *Hydrobiologia* 565:201–216.
- 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.
- Van Noordwijk, C.G.E., J. Kuper, W. Floor-Zwart, K. Alders, H. Turin, T. Heijerman, B. Aukema and H. Siepel. 2012. Knelpunten voor loopkevers, wantsen en sprinkhanen in hellingschraallanden. *Directie Agrokennis, Ministerie van Economische Zaken, Den Haag*.

- Van Noordwijk, C.G.E. and A. Klimkowska. 2013. Profiteren geleedpotigen van maaiselverspreiding in natuurontwikkelingsgebieden? *De Levende Natuur* 114:226–231.
- Van Noordwijk, C.G.E., M. Weijters, N.A.C. Smits, R. Bobbink, L. Kuiters, E. Verbaarschot, R. Versluijs, J. Kuper, W. Floor-Zwart, H.P.J. Huiskes, E. Remke and H. Siepel. 2013. Uitbreiding en herstel van Zuid-Limburgse hellingschraallanden. Eindrapport 2^e fase O+BN onderzoek. Directie Agrokennis, Ministerie van Economische Zaken, Den Haag.
- Van Nouhuys, S. 2005. Effects of habitat fragmentation at different trophic levels in insect communities. *Annales Zoologici Fennici* 42:433–447.
- 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.
- Van Swaay, C.A.M. 2002. The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation* 104:315–318.
- Van Swaay, C.A.M., A. Cuttelod, S. Collins, D. Maes, M.L. Munguira, M. Sasic, J. Settele, R. Verovnik, T. Verstrael, M.S. Warren, M. Wiemers and I. Wynhoff. 2010. European red list of butterflies. Publications Office of the European Union, Luxembourg.
- Van Turnhout, C.A.M., R.P.B. Foppen, R.S.E.W. Leuven, A. Van Strien and H. Siepel. 2010. Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation* 143:173–181.
- Van Turnhout, C.A.M. 2011. Birding for science and conservation, explaining temporal changes in breeding bird diversity in the Netherlands. Ph.D. thesis, Radboud University Nijmegen.
- Van Turnhout, C.A.M., R.S.E.W. Leuven, A.J. Hendriks, G. Kurstjens, A.J. Van Strien, R.P.B. Foppen, H. Siepel. 2012. Ecological strategies successfully predict the effects of river floodplain rehabilitation on breeding birds. *River Research and Applications* 28:269–282.
- 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.
- Vanbergen, A.J., B.A. Woodcock, M. Koivula, J. Niemelä, D.J. Kotze, T. Bolger, V. Golden, F. Dubs, G. Boulanger, J. Serrano, J.L. Lencina, A. Serrano, C. Aguiar, A.-C. Grandchamp, S. Stofer, G. Szél, E. Ivits, P. Adler, J. Markus and A.D. Watt. 2010. Trophic level modulates carabid beetle responses to habitat and landscape structure: a pan-European study. *Ecological Entomology* 35:226–235.
- Vandewalle, M., F. de Bello, M.P. Berg, T. Bolger, S. Doledec, F. Dubs, C.K. Feld, R. Harrington, P.A. Harrison, S. Lavorel, P.M. da Silva, M. Moretti, J. Niemela, P. Santos, T. Sattler, J. P. Sousa, M.T. Sykes, A.J. Vanbergen and B.A. Woodcock. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation* 19:2921–2947.
- Verberk, W.C.E.P. 2008. Matching species to a changing landscape, aquatic macroinvertebrates in a heterogeneous landscape. Ph.D. thesis, Radboud University Nijmegen.
- Verberk, W.C.E.P. 2010. Life-history strategies: a fresh approach to causally link species and their habitat. Pages 137–156 in: De Carlo, F. and A. Bassano (eds.). *Freshwater Ecosystems and Aquaculture Research*. Nova Publishers, New York.
- Verberk, W.C.E.P., H. Siepel and H. Esselink. 2008a. Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology* 53:1722–1738.
- Verberk, W.C.E.P., H. Siepel and H. Esselink. 2008b. Applying life-history strategies for freshwater macroinvertebrates to lentic waters. *Freshwater Biology* 53:1739–1753.
- Verberk, W.C.E.P., R.S.E.W. Leuven, G.A. Van Duinen and H. Esselink. 2010a. Loss of environmental heterogeneity and aquatic macroinvertebrate diversity following large-scale restoration management. *Basic and Applied Ecology* 11:440–449.

- Verberk, W.C.E.P., G. Van der Velde and H. Esselink. 2010b. Explaining abundance-occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. *Journal of Animal Ecology* 79:589–601.
- 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.
- 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.
- Violle, C., M.L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116, 882–892.
- 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.
- Vreysen, M.J.B., K.M. Saleh, M.Y. Ali, A.M. Abdulla, Z.R. Zhu, K.G. Juma, V.A. Dyck, A. R. Msani, 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.
- Wachmann E., A. Melber and J. Deckert. 2004. Wanzen. Band 2. Cimicomorpha, Microphysidae (Flechtenwanzen), Miridae (Weichwanzen). *Die Tierwelt Deutschlands* 75:1–288.
- Wachmann E., A. Melber and J. Deckert. 2006. Wanzen. Band 1. Dipsocoromorpha, Nepomorpha, Gerromorpha, Leptopodomorpha, Cimicomorpha (Teil 1). *Die Tierwelt Deutschlands* 77:1–263.
- Wachmann E., A. Melber and J. Deckert. 2007. Wanzen. Band 3. Pentatomomorpha I. Aradidae, Lygaeidae, Piesmatidae, Berytidae, Pyrrhocoridae, Alydidae, Coreidae, Rhopalidae, Stenocephalidae. *Die Tierwelt Deutschlands* 78:1–272.
- Wachmann E., A. Melber and J. Deckert. 2008. Wanzen. Band 4. Pentatomomorpha II. Pentatomoidea. Cydnidae, Thyreocoridae, Plataspidae, Acanthosomatidae, Scutelleridae, Pentatomidae. *Die Tierwelt Deutschlands* 81:1–230.
- Wagner, T.L., H. Wu, P.J.H. Sharpe, R.M. Schoolfield and R.N. Coulson. 1984. Modeling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America* 77:208–225.
- 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: WallisDeVries, M.F.J., P. Bakker and S.E. Van Wieren (eds.). *Grazing and conservation management*. Kluwer, Dordrecht.
- WallisDeVries, M.F. 2006. Larval habitat quality and its significance for the conservation of *Melitaea cinxia* in Northwestern Europe. Pages 281–294 in: Fartmann, T. and G. Hermann (eds.). *Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa*. Abhandlungen aus dem Westfälischen Museum für Naturkunde.
- WallisDeVries, M.F. and C.A.M. Van Swaay. 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology* 12:1620–1626.

- 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., P. Poschlod and J.H. Willems. 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation* 104:265–273.
- WallisDeVries, M.F., A.E. Parkinson, J.P. Dulphy, M. Sayer 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.
- Waloff, N. 1957. The effect of the number of queens of the ant *Lasius flavus* (Fab.) (Hym., Formicidae) on their survival and on the rate of development of the first brood. *Insectes Sociaux* 4:391–408.
- Waloff, N. 1980. Studies on grassland leafhoppers (Auchenorrhyncha, Homoptera) and their natural enemies. *Advances in Ecological Research* 11:81–215.
- Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J. Fromentin, O.H.I and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Wamser, S., T. Diekötter, L. Boldt, V. Wolters and J. Dauber. 2012. Trait-specific effects of habitat isolation on carabid species richness and community composition in managed grasslands. *Insect Conservation and Diversity* 5:9–18.
- 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.
- Webb, C.T., J.A. Hoeting, G.M. Ames, M.I. Pyne and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* 13:267–83.
- Weiner, J. 1995. On the practice of ecology. *Journal of Ecology* 83:153–158.
- White, P.S. and J.L. Walker. 1997. Approximating nature's variation: Selecting and using reference information in restoration ecology. *Restoration Ecology* 5:338–349.
- White, T.C.R. 1993. The inadequate environment. Nitrogen and the abundance of animals. Springer-Verlag, Berlin.
- Willems, J.H. 2001. Problems, approaches and results in restoration of Dutch calcareous grassland during the last 30 years. *Restoration Ecology* 9:147–154.
- Willems, J.H., R.K. Peet and L. Bik. 1993. Changes in chalk grasland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science* 4:203–212.
- Williams, C.B. 1943. Area and number of species. *Nature* 152:264–267.
- Williams, C.B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. Academic Press, London.
- 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.
- 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.
- With, K.A. and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76:2446–2459.
- With, K.A., R.H. Garner and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:151–169.

- Woodcock, B.A. and R.F. Pywell. 2010. 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., 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., A.R. Edwards, C.S. Lawson, D.B. Westbury, A.J. Brook, S.J. Harris, V.K. Brown and S.R. Mortimer. 2008. Contrasting success in the restoration of plant and phytophagous beetle assemblages of species-rich mesotrophic grasslands. *Oecologia* 154:773–783.
- Woodcock, B.A., A.R. Edwards, C.S. Lawson, D.B. Westbury, A.J. Brook, S.J. Harris, G. Masters, R. Booth, V. K. Brown and S.R. Mortimer. 2010a. The restoration of phytophagous beetles in species-rich chalk grasslands. *Restoration Ecology* 18:638–644.
- 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. 2010b. The role of management and landscape context in the restoration of grassland phytophagous beetles. *Journal of Applied Ecology* 47:366–376.
- 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.
- 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.
- 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.
- Zamora, R. and J.M. Gomez. 1993. Vertebrate herbivores as predators of insect herbivores – an asymmetrical interaction mediated by size differences. *Oikos* 66:223–228.
- 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. *PNAS* 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.



Arthropod eyes (Photo: Theodoor Heijerman)

Summary

Background

Over the past century, a multitude of anthropogenic stressors has led to large-scale biodiversity declines. This is not only detrimental to biodiversity conservation per se, it also poses a serious threat to ecosystem functioning and biodiversity based ecosystem services. In semi-natural habitats like calcareous grasslands, the initial conservation response generally is to revert back to the traditional farming practices that formed these sites in the first place. However, exactly copying traditional methods is seldom feasible for economical, practical and social reasons. Also, traditional farming practices are mostly insufficient to keep up with aerial nitrogen deposition and the nutrient enrichment that has built up in the soil. In addition, the landscape context has changed dramatically, with semi-natural habitats being reduced to small habitat fragments surrounded by intensively managed arable land. To adequately address all of these issues, we need to design new conservation strategies that are effective in dealing with the contemporary environmental pressures and are practically, economically and socially feasible. This requires thorough understanding of the mechanisms shaping biodiversity in semi-natural habitats.

Species' traits have been proposed to give insight in the mechanisms underlying species-environment relationships. Traits determine an individual's fitness and only species whose individuals are adapted to the current environmental pressures will persist. However, traits do not operate independently. Natural selection acts at the individual level and an individual's fitness is determined by the combined effect of all its traits. Traits are interconnected through trade-offs and different traits may act in concert. Due to such context-dependence of trait values it is essential to incorporate trait interactions in the study of species-environment relationships.

Thesis aim

In this thesis, it is investigated how traits and trait-interactions can be used to understand how species are affected by environmental stressors. Arthropods in calcareous grasslands are used as a model system. Calcareous grasslands have a high arthropod species richness due to their extraordinary plant species richness, unique microclimate and potentially varied vegetation structure. Over the past century, the number, size and quality of calcareous grasslands in Northwestern Europe has strongly declined. To counter these negative effects, remaining sites are increasingly managed for nature conservation purposes. Renewed conservation management however, frequently did not result in the anticipated biodiversity recovery, especially for arthropods.

The research questions in this thesis are: 1) To what extent have arthropod communities in Dutch calcareous grasslands been restored over the past two decades of conservation management? 2) How can species' traits and their interactions be used to gain insight in the mechanisms underlying species-environment relationships? 3) How are arthropods in calcareous grasslands affected by environmental stressors, in particular isolation, fragmentation, vegetation structure & microclimate and disturbance caused by grassland management? 4) Which strategies are most effective to restore and conserve arthropod communities in Dutch calcareous grasslands? These questions are addressed in six chapters covering different selections of arthropod taxa.

Changes in arthropod communities following renewed conservation management

To gain better understanding of the effects of renewed management on a wide range of arthropod taxa, pitfall trap data collected in 1988 and 2005 in eight Dutch calcareous grasslands were compared (**chapter 2**). For all seven investigated arthropod groups, considerable species turn-over was found (i.e. the species list per site differed considerably between the two sampling years). However, overall patterns differed markedly between taxonomic groups. Only for spiders, a significantly greater increase in occurrence of characteristic calcareous grassland species than for generalist species was found. Carabid beetle species richness declined while species richness of true bugs and millipedes increased. Also at the regional scale, effects of management on diversity patterns were mixed. These results indicate that the renewed management has had some positive effects. However, it has not led to full recovery of arthropod communities and some groups even continued to decline. This highlights the need to identify remaining bottlenecks and to devise management strategies to tackle them.

Using traits to understand species-environment relationships

Traits have been proposed as a fruitful tool for community ecology, providing mechanistic understanding of species responses to environmental gradients. Most commonly, traits have been used as independent predictors of a species' ability to deal with particular environmental conditions. This approach is used in **chapter 2** where it is demonstrated that such use of traits and other species' characteristics does explain some of the variation in diversity changes. However, results were not consistent across taxonomic groups and the explanatory power was generally low. This is due to the fact that natural selection does not operate on single traits, but on individuals, causing the adaptive value of a specific trait to depend on the other traits possessed by that individual. In addition, trait-environment research has generally focussed on the effect of one specific environmental gradient (e.g. land-use intensity or extreme winter warming). In semi-natural habitats undergoing renewed conservation management, however, many different factors operate simultaneously, which all affect the local species composition. This multitude of stressors can be expected to cause a multitude of responses both within and between taxonomic groups. To gain understanding of the causes of decline and possibilities for restoration of arthropod communities in calcareous grasslands, we thus need an approach that incorporates trait interactions and enables disentangling the effects of multiple stressors. Methods are explored to tackle these issues from the species-end, using life-history strategies, and from the environment end of species-environment relationships.

Combining traits into life-history strategies

Life-history strategies have been presented as a particularly suitable method to incorporate trait interactions and to disentangle the effects of multiple stressors on a community. In this approach species' traits related to the four domains of reproduction, development, dispersal and synchronization are listed and the adaptive value of these trait combinations

is deduced from literature. In **chapter 3**, this life-history strategy approach is applied to ants. This revealed three particular circumstances to which ants are vulnerable, two of which seem limiting in Dutch calcareous grasslands: habitat isolation and microclimatic conditions in summer. The strength of the life-history strategy approach is that it explicitly incorporates trait interactions. It allows to evaluate the relative importance of traits and to weight traits in an informed way, depending on the remainder of a species' biology. This approach is explicitly mechanistic, allowing results to be extrapolated to other (similar) species or circumstances. Another important advantage of the life-history strategy approach is that it draws attention to very specific bottlenecks for the species group under study. Drawbacks of the life-history strategy approach are that it requires extensive knowledge of a species' biology, it lacks fixed guidelines for the adaptive value of a specific trait and there is no fixed level of aggregation. Indeed the compilation of strategies requires extensive knowledge of a species' biology and of the adaptive value of specific trait combinations. This is problematic for some arthropod groups, including even well studied taxa like carabid beetles. Often, little knowledge is available on the development of immature stages, while these are likely to be the most vulnerable. With respect to the lack of fixed adaptive values of specific trait attributes, I argue that ignoring the context dependence of trait values is at least as arbitrary. The absence of fixed adaptive values is not necessarily a problem, as long as hypotheses are firmly rooted in logic combinations of existing biological knowledge. Moreover, derived hypotheses should subsequently be put under scrutiny through rigorous testing of field data (see **chapter 3**). In fact, new hypotheses on the adaptive value of specific trait combinations are essential to derive new insights into the bottlenecks species are encountering in their environments. The criticism that there is no fixed level of aggregation of ecological strategies is to a certain extent legitimate. If we would include all possible traits, each species would be assigned to a separate strategy. This serves no purpose as it does not help to make any generalizations and does not improve predictive power. We thus need to choose an intermediate level of abstraction that includes main traits, but excludes minor differences between species. Choosing which traits to include is to some extent subjective, as there is no single objective level of aggregation above the species level. However, the fact that there is no single fully objective level of aggregation that suits *all* ecological questions, does not mean that there are no appropriate levels of aggregation for *specific* ecological questions.

Exploring environmental filters

Most trait research so far has not started at the species end of species-environment relationships, but rather investigated a single ecological gradient or stressor. This bypasses the difficulties of having to disentangle different environmental stressors from the traits of species present in the local species pool. A natural draw-back is that only stressors which are already deemed important will be investigated, hampering the discovery of new bottlenecks. In **chapter 7** this approach was used to investigate how the importance of calcareous grassland area depends on the trophic rank, habitat affinity and dispersal ability of carabid beetles. My analysis demonstrated that all three species characteristics synergistically affect species' sensitivity to habitat area. While each trait independently had low predictive power, together they show that species which are both zoophagous

and characteristic for calcareous grasslands respond strongly to calcareous grassland area. Thus, also when investigating single environmental factors, it is crucial to incorporate trait interactions. An advantage of starting at the environment end of species-environment relationships is that the specific stressor under study gives clear guidelines as to the circumstances to which adaptations are needed. This focuses the search for relevant traits and adaptations and makes it unnecessary to investigate a species' entire life-history. While being a great advantage, this clear focus also holds a potential risk. Analyses will generally be limited to the most obvious traits, while seemingly unrelated traits may alter species' responses as well. In **chapter 6** it is, for example, demonstrated that a species' spread rate through fragmented landscapes is not only affected by a species' dispersal traits, but also by its traits related to reproduction and development.

Through arthropod eyes

Ultimately, understanding the match between species' life-cycles and environmental assembly filters requires knowledge of both. This means that the two approaches described above, i.e. the ecological strategy approach and the exploration of environmental filters, should ideally be integrated into one iterative process. A fruitful way to do this is to view the environment 'through an arthropod's eyes'. Analysing a species' life-cycle and comparing each stage against the environment in which it occurs, highlights both the challenges that must be overcome and to what extent the species has trait attributes to do so. This approach is similar to the construction of ecological strategies but it is more flexible, using all available information (morphological, physiological and phenological traits, life-history traits and behavioural responses). The sheer number of potential environmental stressors makes it nearly impossible to construct fixed ecological strategies (i.e. groups of species that respond similarly to all aspects of their environment) that can be applied in any context. The limited knowledge on many aspects of arthropod life-cycles only adds to this problem. Therefore, evaluating species' life-cycles in relation to specific environmental stressors may be more effective. This does not mean that there are no general patterns. Species-environment relationships found for a specific set of species in a specific environment can still be extrapolated to other species or circumstances. However, there is no single limited set of traits that explains the presence or absence of a set of species under all circumstances. Researchers should therefore evaluate critically whether pre-existing classifications are relevant in the light of their particular research question. There are several advantages of systematically analyzing an arthropod's life-cycle in the way described above. Like the strategy approach, it draws attention to trait interactions (as the entire life-cycle is evaluated) and it explicitly incorporates immature stages. In addition, this approach uses all available knowledge on various levels. The main pitfall is that it lacks a fixed structure and may lead to unfounded, descriptive studies that bear little predictive power. To gain structure, the aim of finding mechanistic understanding and to retrieve testable hypotheses should be used as a 'compass' to guide which information to incorporate in the life-cycle analyses. To gain predictive power, life-cycles should be compared between species. In line with the strategy approach, species can then be grouped according to their predicted response to the specific environmental stressor(s) under study. Hypotheses derived from such life-cycle analyses should then be rigorously tested before further implementation.

Advancements in species-environment relationships

Using the methods evaluated above, the research presented in this thesis has revealed several new insights into species-environment relationships. In **chapter 3**, it was discovered that microclimatic conditions are particularly important for ant species exhibiting claustral colony founding (i.e. with queens feeding the first batch of workers from their own fat reserves). Soil temperatures are, however, only limiting for species that are constrained in their development time due the combined effect of a number of traits relating to colony founding and larval development. For these species, specifically the soil temperature in summer and autumn is crucial for colony founding. In **chapter 4**, a literature review was carried out to summarize all known effects of grazing on arthropod diversity. This revealed that arthropod species richness is generally more sensitive to grazing than plant species richness. In **chapter 5**, it was demonstrated experimentally that autumn and winter grazing can pose a serious threat to hibernating butterfly larvae. Grazing intensity proved an important factor determining larval mortality rates. **Chapter 6** highlighted that species persistence and dispersal in fragmented landscapes does not only depend on dispersal traits, but also on population vital rates like age at maturity and carrying capacity. In **chapter 7**, it was demonstrated that trophic level, habitat affinity and dispersal ability synergistically affect species' sensitivity to habitat area. In addition, this study indicates that the effect of trophic level is independent of a species degree of food specialization. In all, these results demonstrate that effective conservation of arthropod communities calls for both optimization of the management regime within calcareous grassland reserves and addressing issues of habitat isolation and fragmentation in the wider landscape. A summary of the specific bottlenecks operating on Dutch calcareous grasslands is given below, followed by management recommendation to deal with them.

Bottlenecks for arthropods in Dutch calcareous grasslands

The current management regime in most Dutch calcareous grasslands, consisting of intensive grazing or mowing in autumn, has proven to be insufficient to create an open vegetation structure and warm microclimate in summer for characteristic ant species under current nutrient levels (**chapter 3**). It also leads to high mortality rates among overwintering caterpillars (**chapter 5**). In addition to these management related bottlenecks, arthropod conservation is hindered by the small size of single sites, a lack of habitat heterogeneity and a lack of functional connectivity between sites.

The largest Dutch calcareous grasslands measure just a few hectares, which proved too small for zoophagous, characteristic calcareous grassland carabid beetles (**chapter 7**). Also, zoophagous, characteristic calcareous grassland carabid beetles with better flight ability only remain present in the largest sites. Calcareous grassland size thus is a limiting factor for part of the characteristic arthropod fauna in Dutch calcareous grasslands. The fact that zoophagous species proved more vulnerable to site size than phytophagous species implies that in addition to biodiversity loss per se, trophic interactions may be seriously disrupted in sites smaller than 5 hectares.

Habitat heterogeneity in calcareous grasslands and neighbouring vegetation types adds significantly to arthropod diversity. On a small scale, habitat heterogeneity in the form

of various vegetation structures and patches of bare ground is essential for many characteristic arthropod species to complete their life-cycle. On a larger scale, availability of calcareous grassland differing in slope and aspect in close proximity, provides a buffer against extreme weather conditions. Intensive management that is carried out once a year throughout an entire site diminishes small-scale habitat heterogeneity. Large-scale heterogeneity is currently scarce due to habitat fragmentation and isolation.

In the current landscape, containing approximately 1% calcareous grassland, functional connectivity across the landscape is virtually non-existent, even for species with good dispersal ability (**chapter 6**). Some dispersal over shorter distances occurs among good dispersers, but poor dispersers are strongly limited in their occurrence (**chapter 3**). For carabid beetles the positive effect of additional calcareous grassland in the surrounding landscape on population persistence is limited to 500 metres (**chapter 7**). These results demonstrate that arthropod communities in many existing sites are not part of a meta-population structure, putting them at greater risk of local extinction.

Management recommendations

An open vegetation structure and warm microclimate in summer can be created by shifting the main management period to late spring or early summer. Some reserves are already grazed in summer with positive effects on microclimatic conditions and the presence of characteristic ant species (**chapter 3**). Summer management could also address high caterpillar mortality caused by intensive autumn management and it is expected to be more effective in removing excess nutrients. Summer management may, however quickly result in new bottlenecks, as food sources for pollinators will be depleted and characteristic plant species will be consumed before seed set. Spreading management intensity in time and space, with a rotational grazing regime, allowing sufficient vegetation regrowth between grazing rounds, seems most effective to restore both plant and arthropod diversity (**chapter 4**). To enhance habitat heterogeneity the management intensity should be varied to enhance existing heterogeneity within sites and to create small scale structures, specifically patches of bare ground. Rotational management provides good opportunities to create such variation in management intensity. A rotational grazing regime is thus likely to improve arthropod biodiversity and specifically survival chances for characteristic calcareous grassland arthropods. However, full recovery seems impossible under current nutrient levels. Obtaining an optimal vegetation structure for arthropod conservation under current soil nutrient levels, requires intensive management, which quickly becomes detrimental to overall arthropod diversity (**chapter 4**). The only solution to this dilemma between grass- and scrub encroachment, resulting from insufficient management, and too much disturbance, under more intensive management, is to drastically lower soil nutrient levels and hence nitrogen deposition.

The area needed for viable populations increases with increasing environmental variability and increased occurrence of catastrophic events. Habitat variability and the occurrence of catastrophic events can be expected to increase in calcareous grasslands due to climate change and high soil nutrient levels. To increase resilience of arthropod populations to current and future global change, increasing the size of single sites beyond the 5 hectare threshold should receive top priority. In addition, long-term species persistence

will increase with increased availability of calcareous grassland sites in the landscape (**chapter 6**). Efforts should focus on increasing calcareous grassland availability within a few hundred metres of existing sites (**chapters 3, 6 and 7**). Even over such short distances targeted reintroduction, similar to green hay application for plants, is expected to dramatically improve restoration success for many arthropod species.

Integrating requirements of arthropods and plants

Evidence is mounting that restoration of plant communities does not ensure improvement of arthropod communities. In fact, arthropod diversity is more sensitive than plant diversity, certainly when it comes to grazing management (**chapter 4**), but most likely also to habitat size (**chapter 7**) and global change in general. Management strategies thus need to integrate the requirements of plants and arthropods to preserve arthropod biodiversity and the important ecosystem services provided by them. This has often been viewed as a daunting task because even among arthropods there are large differences in performance under conservation management (**chapter 2**), potentially leading to conflicting management recommendations. The research in this thesis has uncovered a number of different (previously unknown) bottlenecks within calcareous grassland reserves for different taxonomic groups. Previous studies on plants found again other bottlenecks, in particular, insufficient nutrient removal. However, these different bottlenecks do not present an inherent conflict when it comes to appropriate management strategies. The management recommendations given above address all uncovered bottlenecks in an integrated way. This integration of requirements was achieved due to understanding of the mechanisms underlying species responses to environmental stressors. Knowing what specific requirements different species have, allows to fit the requirements of different taxa together. This highlights the need for increased mechanistic understanding of how arthropods respond to their environment and increased attention for these requirements in conservation policy and management.

The jumping spider *Evarcha arcuata* (Photo: Aart Noordam)



Samenvatting

Achtergrond

Antropogene invloeden hebben in de afgelopen eeuw geleid tot een sterke afname van de biodiversiteit. Deze afname vormt niet alleen een bedreiging voor het voortbestaan van de rijkdom aan levensvormen op aarde, maar kan bovendien verstrekende gevolgen hebben voor het functioneren van ecosystemen en de de onmisbare diensten die deze systemen leveren. Inmiddels worden op diverse plekken pogingen gedaan om de achteruitgang in biodiversiteit te stoppen door bescherming en herstel van natuur. In half-natuurlijke ecosystemen, zoals kalkgraslanden, wordt dit meestal gedaan door herinvoering van het oorspronkelijke beheer dat leidde tot het ontstaan van deze ecosystemen. Het exact kopiëren van traditionele beheervormen is echter zelden mogelijk om praktische, sociale en economische redenen. Daarnaast biedt dit beheer onvoldoende tegenwicht aan de toegenomen atmosferische stikstofdepositie en de gevolgen van jarenlange verwaarlozing. Daar komt bij dat de landschappelijke context sterk is veranderd: Waar een eeuw geleden half-natuurlijke ecosystemen nog een groot deel van het agrarische landschap innamen, is hun oppervlakte nu gereduceerd tot sterk geïsoleerde snippers, ingesloten door intensieve landbouw. Om de biodiversiteit effectief te beschermen zijn nieuwe beheerstrategieën nodig, die een antwoord bieden op al deze bedreigingen en daarnaast ook praktisch uitvoerbaar en economisch haalbaar zijn. Het ontwerpen van dergelijke beheerstrategieën vergt inzicht in de mechanismen die ten grondslag liggen aan de biodiversiteit in half-natuurlijke ecosystemen. Soorteigenschappen lijken een geschikt instrument te zijn om inzicht te krijgen in deze mechanismen. Immers, alleen individuen die voldoende zijn aangepast aan het heersende milieu kunnen overleven. Dit betekent dat de eigenschappen van lokaal voorkomende soorten zijn gekoppeld aan de heersende omgevingsfactoren. Soorteigenschappen zijn echter niet onafhankelijk van elkaar ontstaan. Natuurlijke selectie speelt zich af op het niveau van het individu en de fitness van een individu wordt bepaald door het gecombineerde effect van alle eigenschappen samen. Hierdoor is het essentieel de samenhang tussen eigenschappen mee te wegen bij het bestuderen van de relaties tussen soorten en hun omgeving.

Doel

In dit proefschrift wordt beschreven hoe soorteigenschappen en hun onderlinge samenhang inzicht kunnen geven in de relatie tussen soorten en hun omgeving. Ongewervelden in kalkgraslanden zijn hierbij gebruikt als voorbeeldsysteem. Kalkgraslanden zijn in potentie zeer rijk aan insecten en andere ongewervelden, onder meer door de hoge plantensoortenrijkdom, het warme en gevarieerde microklimaat en de variatie in vegetatiestructuur. Het areaal kalkgrasland in Noordwest Europa is de afgelopen eeuw sterk achteruit gegaan. In de overgebleven gebieden wordt in toenemende mate natuurbeheer uitgevoerd. Dit beheer heeft echter niet overal geleid tot het verwachte herstel van soortenrijkdom.

De onderzoeksvragen die in dit proefschrift worden behandeld zijn: 1) In welke mate heeft de afgelopen twee decennia kalkgraslandbeheer geleid tot herstel van de karakteristieke ongewervelden gemeenschappen in de Zuid-Limburgse kalkgraslanden? 2) Hoe kunnen soorteigenschappen en hun interacties inzicht geven in de relaties tussen

soorten en hun omgeving? 3) Hoe worden ongewervelden in kalkgraslanden beïnvloed door omgevingsfactoren, met name: terreinisolatie, versnippering, vegetatiestructuur & microklimaat en verstoring veroorzaakt door het gevoerde natuurbeheer? 4) Welke herstelstrategieën zijn het meest effectief voor herstel van karakteristieke gemeenschappen van ongewervelden in Nederlandse kalkgraslanden? Deze vragen worden behandeld in 6 hoofdstukken aan de hand van onderzoek naar verschillende groepen ongewervelden.

Veranderingen in arthropodengezelschappen na herinvoering van kalkgraslandbeheer

Om inzicht te krijgen in de effecten van hernieuwd kalkgraslandbeheer op ongewervelden zijn potvalvangsten die werden verzameld in 1988 en 2005 met elkaar vergeleken (**hoofdstuk 2**). De soortensamenstelling was voor alle zeven onderzochte groepen aanzienlijk veranderd, maar de gevonden patronen varieerden sterk. Alleen onder de spinnen was er een significant grotere toename aan karakteristieke kalkgraslandsoorten dan aan overige soorten. De loopkever soortenrijkdom nam significant af, terwijl de soortenrijkdom aan wantsen en miljoenpoten toenam. Ook op regionaal niveau waren er grote verschillen in de ontwikkeling van diversiteitspatronen. De resultaten laten zien dat sommige groepen vooruit zijn gegaan sinds de herinvoering van het kalkgraslandbeheer, maar dat andere groepen niet hebben geprofiteerd of zelfs verder achteruit zijn gegaan. Om verder herstel te bewerkstelligen moet achterhaald worden welke knelpunten herstel in de weg staan en met welke beheervormen deze opgelost kunnen worden.

Soorteigenschappen

Analyses van soorteigenschappen zijn regelmatig ingezet om inzicht te krijgen in de relatie tussen soorten en hun omgeving. Tot nu toe werden hiervoor eigenschappen als onafhankelijke factoren geanalyseerd. In **hoofdstuk 2** is dit ook gedaan, in de hoop inzicht te krijgen in de factoren die bepalen welke soorten na herinvoering van het beheer voor- of juist achteruit gingen. Een aantal eigenschappen bleek een significant effect te hebben op de verandering in het voorkomen van soorten. Het verklarend vermogen van deze losse eigenschappen was echter zeer laag en de patronen varieerden sterk tussen de geanalyseerde soortgroepen. Dit komt omdat eigenschappen niet onafhankelijk van elkaar opereren; de daadwerkelijke effect op de fitness van een eigenschap hangt af van de overige eigenschappen van hetzelfde individu. Bovendien spelen in half-natuurlijke systemen een groot aantal processen tegelijkertijd, die zorgen voor net zoveel verschillende veranderingen in soortensamenstelling die tegelijkertijd tot uiting komen. In de volgende hoofdstukken zijn methoden ontwikkeld om deze twee tekortkomingen van traditionele eigenschap-analyses het hoofd te bieden. Dit is gedaan vanuit het perspectief van de soort, met behulp van levensstrategieën, en vanuit het omgevingsperspectief, door één specifieke omgevingsfactor te analyseren.

Levensstrategieën

Het formuleren van levensstrategieën is bij uitstek geschikt om rekening te houden met interacties tussen soorteigenschappen. De levensstrategie van een soort is het gecombineerde effect van alle eigenschappen die te maken hebben met reproductie, ontwikkeling, dispersie en synchronisatie. In **hoofdstuk 3** zijn dergelijke levensstrategieën geformuleerd voor de in kalkgrasland voorkomende mierensoorten. Uit de analyse van vangstgegevens in combinatie met de levensstrategieën bleek dat mieren met name gevoelig zijn voor terreinisolatie en te lage bodemtemperaturen in de zomer.

Het grootste voordeel van deze methode is dat direct inzicht wordt verkregen in de mechanismen die verantwoordelijk zijn voor de respons van soorten op het milieu. Bovendien wordt meteen duidelijk welke omgevingsfactoren het belangrijkste zijn voor de betrokken taxonomische groep. Een nadeel van deze aanpak is dat veel kennis vereist is over de biologie van alle betrokken soorten en over de ecologische gevolgen van deze eigenschappen. Bovendien staat niet vooraf vast tot welk niveau strategieën moeten worden gedefinieerd en hebben eigenschappen in deze aanpak geen vaste waarde – het nut van een eigenschap hangt af van andere eigenschappen van dezelfde soort. De grote hoeveelheid biologische en ecologische kennis die vereist is voor het opstellen van levensstrategieën is een knelpunt in de daadwerkelijke toepassing. Met name kennis over de ontwikkeling van larvale stadia ontbreekt voor veel soorten. Het gebrek aan een vaste (adaptieve) waarde van individuele eigenschappen is geen onoverkomelijk probleem, zolang hypothesen worden opgesteld op basis van (combinaties van) bewezen biologische verbanden en vervolgens worden getoetst met behulp van onafhankelijke velddata (zie **hoofdstuk 3**). Door het gebrek aan een vaste (adaptieve) waarde van eigenschappen kunnen levensstrategieanalyses juist een belangrijke bijdrage leveren aan de ontwikkeling van nieuwe kennis over de relatie tussen soorten en hun omgeving. De kritiek dat er niet één vooraf vastgesteld niveau is tot waar strategieën moeten worden opgesplitst is deels terecht. Echter, het feit dat er niet één duidelijk splitsingsniveau is dat geschikt is voor beantwoording van *elke* ecologische vraag, wil niet zeggen dat er geen geschikt splitsingsniveau is voor *specifieke* ecologische vragen.

Analyse van omgevingsfactoren

Het leeuwendeel van gepubliceerde onderzoeken dat gebruik maakt van soorteigenschappen gaat niet uit van het soortsperspectief, maar neemt één specifieke omgevingsfactor of één gradiënt als vertrekpunt. Met deze aanpak worden de moeilijkheden omzeild die het ontrafelen van het effect van verschillende omgevingsfactoren met zich meebrengt. Daar staat tegenover dat slechts inzicht wordt verkregen in het effect van vooraf bekende stressoren. In **hoofdstuk 7** is deze aanpak gebruikt om inzicht te krijgen in welke mate het belang van terreingrootte voor loopkevers afhangt van trofisch niveau, habitat affiniteit en vliegvermogen. Deze analyse liet zien dat de drie genoemde eigenschappen en soortkarakteristieken samen bepalen hoe gevoelig soorten zijn voor de factor terreingrootte. Alleen soorten die zowel carnivoor zijn als karakteristiek voor kalkgraslanden zijn in hun voorkomen beperkt tot grote terreinen. Dit illustreert dat

het belangrijk is de interacties tussen eigenschappen te analyseren, ook als slechts één omgevingsfactor tegelijk geanalyseerd wordt.

Het analyseren van slechts één omgevingsfactor heeft als belangrijk voordeel dat het duidelijk is welke eigenschappen in de analyse meegenomen moeten worden en tot op welk niveau soorten moeten worden opgesplitst. Kennis over de gehele levenscyclus van een soort is voor deze analyse dus niet noodzakelijk. Door direct in te zoomen op eigenschappen waarvan bekend is dat zij de respons van soorten op de onderzochte omgevingsfactor beïnvloeden, blijven onontdekte relaties met minder voor de hand liggende eigenschappen echter onopgemerkt. In **hoofdstuk 6** wordt bijvoorbeeld aangetoond dat de snelheid waarmee een soort zich verspreid door een versnipperd landschap niet alleen afhangt van voor de hand liggende eigenschappen als vliegvermogen en honkvastheid, maar ook wordt beïnvloed door eigenschappen die te maken hebben met reproductie en ontwikkeling.

Door insectenogen

Kennis over zowel omgevingsfactoren als levenscyclus van soorten is nodig om te begrijpen hoe het voorkomen van soorten wordt bepaald door het milieu. Dit betekent dat uiteindelijk de twee bovengenoemde aanpakken, het formuleren van levensstrategieën en analyse van omgevingsfactoren, geïntegreerd moeten worden. Een intuïtieve manier om dit te doen is om ‘door insectenogen’ de omgeving te bekijken. Het doornemen van de levenscyclus van een soort in relatie tot zijn omgeving gedurende elke levensfase, geeft gerichte informatie over mogelijke knelpunten die de soort ondervindt. Een dergelijke analyse geeft ook inzicht in de aanpassingen die een soort ontwikkeld kan hebben om met deze knelpunten om te gaan. Deze aanpak is vergelijkbaar met het opstellen van levensstrategieën, maar flexibeler, omdat gebruik gemaakt wordt van alle beschikbare informatie. Bovendien wordt het detailniveau van opsplitsing van de strategieën op deze manier afgestemd op de specifieke situatie die wordt onderzocht. Het bekijken van de omgeving ‘door insectenogen’ legt, evenals de levenstrategieaanpak, de nadruk op interacties tussen eigenschappen en neemt eisen van onvolwassen stadia expliciet mee. In tegenstelling tot de levenstrategieaanpak wordt echter niet langer uitgegaan van vaste strategieën die in elke context van toepassing zijn, want door de grote verscheidenheid aan potentiële omgevingsfactoren is dit nauwelijks uitvoerbaar. De afwezigheid van vaste strategieën betekent niet dat er geen algemene patronen zijn, of dat reeds bekende relaties tussen soorten en hun omgeving niet doorvertaald kunnen worden naar andere systemen of soorten. Onderzoekers moeten steeds kritisch bekijken of reeds bestaande classificaties relevant zijn voor hun specifieke studiesysteem en onderzoeksvraag.

Om te voorkomen dat deze aanpak slechts leidt tot beschrijvende analyses met een beperkt voorspellend vermogen, dient nadrukkelijk gezocht te worden naar de mechanismen die de respons van soorten op hun omgeving veroorzaakt. Bovendien is het aan te bevelen net als in de levenstrategieaanpak, soorten met een vergelijkbare respons te groeperen en gezamenlijk te analyseren. Tot slot moeten de opgestelde hypothesen getoetst worden met onafhankelijk verkregen (veld)data.

Nieuwe inzichten in de eisen die soorten stellen aan hun omgeving

Door toepassing van de hierboven beschreven methodes heeft dit onderzoek een aantal nieuwe inzichten opgeleverd met betrekking tot de eisen die soorten stellen aan hun omgeving. In **hoofdstuk 3** is aangetoond dat mieren waarvan jonge koninginnen de eerste werksters voeren vanuit hun eigen vetreserves (claustrale koloniestichting) zeer gevoelig zijn voor een te lage bodemtemperatuur, met name in de (na)zomer. Dit geldt alleen voor soorten die een beperkte ontwikkelingstijd hebben voor hun eerste werksters op grond van het gecombineerde effect van meerdere eigenschappen die te maken hebben met de larvale ontwikkeling en de synchronisatie van de levenscyclus. **Hoofdstuk 4** laat zien dat soortenrijkdom van arthropoden over het algemeen gevoeliger is voor begrazing dan plantendiversiteit. In **hoofdstuk 5** is experimenteel aangetoond dat intensieve herfst- en winterbegrazing een ernstige bedreiging kan vormen voor overwinterende rupsen. Dat dispersie en overleving van soorten in een sterk versnipperd landschap niet alleen afhangen van de landschapskarakteristieken en de dispersie-eigenschappen van de betrokken soorten, maar ook van hun ontwikkelings- en reproductie eigenschappen, is aangetoond in **hoofdstuk 6**. In **hoofdstuk 7** is beschreven dat de mate waarin loopkevers afhankelijk zijn van grote terreinen afhangt van hun gecombineerd dispersievermogen, habitataffiniteit en trofische niveau. Voedselspecialisatie lijkt hierbij een beperktere rol te spelen dan tot nu toe werd gedacht. Deze resultaten samen laten zien dat voor herstel en behoud van karakteristieke ongewerveldengemeenschappen in kalkgraslanden zowel verbetering van het interne beheer als vermindering van de versnippering en terreinisolatie noodzakelijk zijn. Hieronder zijn de specifieke knelpunten die zijn gevonden voor de Zuid-Limburgse kalkgraslanden en de beheeraanbevelingen die daar uit voortvloeien samengevat.

Knelpunten in Zuid-Limburgse kalkgraslanden

Het huidige beheerregime in de meeste Zuid-Limburgse kalkgraslanden bestaat uit relatief intensief graas- of maaibeheer, uitgevoerd in het najaar. Dit beheer bleek in de zomer een onvoldoende open vegetatiestructuur en een te koel microklimaat te creëren voor mieren (**hoofdstuk 3**). Tegelijkertijd bleek dit beheer te verstrend voor overwinterende rupsen (**hoofdstuk 5**). Daarnaast zijn de Zuid-Limburgse kalkgraslanden te klein, te geïsoleerd en te homogeen voor optimaal herstel van de ongewervelde fauna. De grootste aaneengesloten kalkgraslanden in Zuid-Limburg zijn slechts enkele hectare groot. Dit blijkt amper groot genoeg te zijn voor behoud van populaties goed vliegende, carnivore, karakteristieke kalkgraslandloopkevers (**hoofdstuk 7**). Slecht vliegende, karakteristieke, carnivore loopkevers zijn zelfs geheel uit de Zuid-Limburgse terreinen verdwenen. Dit heeft niet alleen gevolgen voor de soortenrijkdom, maar kan ook serieuze consequenties hebben voor het functioneren van het complete ecosysteem in terreinen kleiner dan 5 ha.

Habitatheterogeniteit is een belangrijke omgevingsfactor voor de soortenrijkdom van ongewervelden. Op klein schaalniveau is habitatheterogeniteit in de vorm van kale plekken en afwijkende vegetatiestructuren essentieel voor het succesvol doorlopen van de levenscyclus van diverse ongewervelden. Op groter schaalniveau kan variatie in hellingshoek, oriëntatie en beheermoment schuilmogelijkheden bieden tijdens extreme weercondities. Intensief beheer dat in een heel terrein tegelijk wordt uitgevoerd leidt tot

vermindering van de heterogeniteit op kleine schaal. Grootschalige terreinheterogeniteit ontbreekt momenteel bijna volledig door de hoge mate van versnippering en isolatie van kalkgraslandterreinen.

In het huidige landschap, dat voor ongeveer 1% bestaat uit kalkgrasland, is er vrijwel geen uitwisseling van ongewervelden tussen gebieden, zelfs niet bij soorten met goed ontwikkeld vliegvermogen (**hoofdstuk 6**). Slecht verspreidende soorten zijn nu al sterk beperkt in hun voorkomen door de hoge mate van terreinisolatie (**hoofdstuk 3**). Voor loopkevers bleek aanvullend kalkgrasland in de omgeving een positief effect te hebben op de lokale soortenrijkdom, maar dit effect was beperkt tot een straal van 500 meter (**hoofdstuk 7**). Dit laat zien dat de ongewerveldengemeenschappen in de meeste Zuid-Limburgse terreinen geen deel uitmaken van een metapopulatiestructuur en daardoor een verhoogd risico lopen om lokaal uit te sterven.

Beheeraanbevelingen

Door de belangrijkste beheerperiode te verschuiven van herfst naar voorjaar en zomer kan een open vegetatiestructuur en warm microklimaat in de zomer worden bewerkstelligd. In een aantal gebieden wordt al in de zomer begraaasd, wat positieve effecten heeft op de karakteristieke mierenfauna (**hoofdstuk 3**). Zomerbegrazing zou ook uitkomst kunnen bieden voor de hoge sterfte onder overwinterende rupsen en kan leiden tot een hogere nutriëntenafvoer, wat gunstig is voor de karakteristieke flora. Zomerbegrazing kan echter ook leiden tot nieuwe knelpunten, zoals gebrek aan voedsel voor bestuivers en een verminderde zaadzetting van planten. Een gefaseerd beheer, waarbij elk terrein in meerdere fases wordt begraaasd en waarbij voldoende tijd tussen de begrazingsrondes zit om hergroei en herbloei van de vegetatie te krijgen, lijkt het meest effectief voor herstel en behoud van zowel flora als fauna (**hoofdstuk 4**). Daarbij kan de terreinheterogeniteit worden vergroot door de beheerintensiteit binnen het terrein te variëren, zodat lokaal kale plekken en dichtere vegetatiestructuren ontstaan.

Hoewel gefaseerd beheer goede kansen biedt voor verbetering van de omgevingscondities voor ongewervelden in kalkgraslanden, is volledig herstel onmogelijk onder de huidige stikstofemissies. De beheerintensiteit die nodig is om onder de huidige atmosferische depositiewaardes een optimale vegetatiestructuur voor ongewervelden te creëren, heeft onherroepelijk een verstorend effect op een deel van de ongewervelde fauna (**hoofdstuk 4**). De enige uitweg uit dit dilemma – vergrassing als gevolg van onvoldoende beheer of verhoogde mortaliteit onder ongewervelden veroorzaakt door intensiever beheer – is verlaging van de nutriënteniveaus in de bodem. Dit vereist een drastische verlaging van de atmosferische stikstofdepositie.

De terreingrootte die nodig is voor het instandhouden van levensvatbare populaties neemt toe naarmate de temporele variatie in milieuomstandigheden groter wordt. Klimaatscenario's laten zien dat een toename in extreme (weers)omstandigheden zeer waarschijnlijk is. Dit betekent dat vergroting en verbinding van de huidige kalkgraslandreservaten de hoogste prioriteit moet krijgen (**hoofdstuk 6**). Uitbreiding van het areaal kalkgrasland is het meest effectief binnen een straal van 500 meter rond

bestaande kalkgraslanden. Zelfs bij dergelijke korte afstanden is het aan te bevelen gericht ongewervelden te herintroduceren, zoals nu al gebeurt voor planten.

Integratie van beheer voor planten en ongewervelden

Een groot aantal studies heeft inmiddels uitgewezen dat herstelbeheer gericht op planten niet noodzakelijkerwijs goed uitpakt voor ongewervelden. In het algemeen zijn ongewervelden gevoeliger dan planten voor begrazingsbeheer (**hoofdstuk 4**), verminderde terreingrootte (**hoofdstuk 7**) en klimaatverandering. Om ongewervelden en alle ecosysteemdiensten die zij vervullen effectief te beschermen, moet bij het ontwerpen van nieuwe beheerstrategieën expliciet rekening gehouden worden met de eisen die ongewervelden stellen aan hun omgeving. Dit wordt door velen gezien als een haast onmogelijke taak, aangezien de verschillende eisen die planten en groepen ongewervelden stellen aan hun omgeving kunnen leiden tot tegenstrijdige beheeradviezen. Het onderzoek in dit proefschrift heeft inderdaad aangetoond dat verschillende taxonomische groepen andere knelpunten ondervinden. Dit hoeft echter niet te leiden tot tegenstrijdige beheeradviezen. Alle blootgelegde knelpunten worden op een geïntegreerde manier aangepakt met de hierboven voorgestelde beheerwijzigingen. Deze integratie is mogelijk doordat het onderzoek kennis gegenereerd heeft over de mechanismen die verantwoordelijk zijn voor de respons van soorten op hun omgeving. Doordat precies bekend is welke eisen soorten aan hun omgeving stellen, is het mogelijk deze verschillende eisen te integreren. Dit onderschrijft dat het vergroten van onze kennis over de mechanismen die verantwoordelijk zijn voor de respons van ongewervelden op hun omgeving, essentieel is voor effectief ecosysteemherstel.



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The author (Photo: Martijn Anthéunis)

Curriculum Vitae

List of publications

Catharina Gesina Elisabeth van Noordwijk werd geboren in Smithtown (VS) op 9 februari 1981 en kreeg de roepnaam Toos. Samen met haar ouders, zus en broer verhuisde zij diverse malen, onder meer voor een verblijf van zeven jaar in het Zwitserse dorp Ettingen. Terug in Nederland bezocht Toos scholengemeenschap het Pantarijn in Wageningen, waar zij in 1999 haar VWO diploma behaalde. Datzelfde jaar startte ze met een brede, internationale honours opleiding aan University College Utrecht, die in 2002 werd afgesloten met een cum laude Bachelor of Science diploma. Inmiddels was Toos een actief lid geworden van de Nederlandse Jeugdbond voor Natuurstudie (NJN). Vanaf 1994 bekleedde ze diverse bestuursfuncties op afdelings-, districts en landelijk niveau en leidde zij excursies en kampen in de natuur. In 2002 maakte zij deel uit van het landelijke hoofdbestuur als coordinator natuurzaken. In januari 2003 begon Toos met de Master opleiding Biologie aan Universiteit Utrecht. Deze bestond onder meer uit onderzoek naar competitie tussen werksters en koninginnen in hommelmkolonies (afdeling Ethologie, Universiteit Utrecht) en een onderzoek naar de ruimtelijke verspreiding van strandkrabben in de Waddenzee (Nederlands Instituut voor Onderzoek der Zee, Texel). Eind 2004 behaalde Toos haar diploma Master of Biology. In de tussentijd begeleidde Toos als studentassistent diverse cursussen voor de opleiding Biologie en werkte zij als 'jeugdlaborant' in het Utrechts Universiteitsmuseum waar zij bezoekers en schoolklassen rondleidde.

In maart 2005 kwam Toos in dienst van Stichting Bargerveen en begon zij met onderzoek naar fauna in Zuid-Limburgse kalkgraslanden. Naast toegepast projectwerk volgde zij een promotietraject onder begeleiding van prof. Henk Siepel verbonden aan Radboud Universiteit Nijmegen. In 2008 trad Toos toe tot het deskundigenteam Heuvelland voor het O+BN programma van het toenmalige Ministerie voor Landbouw, Natuur en Visserij. Datzelfde jaar trouwde zij met Martijn Antheunisse en in september werd hun eerste dochter - Noor - geboren. Na het plotselinge overleiden van Hans Esselink (oprichter en directeur van Stichting Bargerveen) trad Toos in 2009 toe tot het managementteam van Stichting Bargerveen. Inmiddels werkte zij als senior onderzoeker aan het opzetten en uitvoeren van diverse projecten in het Zuid-Limburgse heuvelland. In 2010 werd tweede dochter - Karlijn - geboren. Begin 2011 legde Toos zich weer toe op het realiseren van haar promotieambities en trok zij prof. dr. Dries Bonte, dr. Matty Berg en dr. Eva Remke aan als (externe) begeleiders. Later dat jaar wist zij succesvol een beurs in de wacht te slepen voor een gemeenschappelijk promotietraject met Universiteit Gent, België. In 2012 combineerde Toos werk aan haar proefschrift met projectwerk voor Stichting Bargerveen en werden de eerste twee artikelen gepubliceerd. Begin 2013 verhuisde Toos met haar gezin naar Urchfont in Engeland. Na drie maanden werk op afstand voor Stichting Bargerveen, trad zij in dienst van Radboud Universiteit Nijmegen om zich volledig te concentreren op het afronden van haar proefschrift. Vanuit huis, met zicht op Salisbury plain, het grootste kalkgrasland van Europa, schreef Toos de laatste vijf hoofdstukken van haar proefschrift; het complete manuscript werd in februari 2014 ingeleverd bij de beoordelingscommissie.

Inmiddels is Toos werkzaam als parttime 'community engagement officer' voor Wiltshire Wildlife Trust. Daarnaast werkt zij als veldassistent voor Liverpool University, verricht zij advieswerk voor diverse instanties en is zij bezig met het opzetten van een onderzoeksproject naar biodiversiteit in volkstuinen in samenwerking met Bristol University.

International peer-reviewed journals

- Van Klink, R., F. van der Plas, C.G.E. van Noordwijk, M.F. WallisDeVries and H.Olff. 2014. Effects of large herbivores on grassland arthropod diversity. *Biological Reviews Online* early DOI: 10.1111/brv.12113.
- 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.
- 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.
- Smallegange, I., C.G.E. van Noordwijk, J. van der Meer and H. van der Veer. 2009. Spatial distribution of shore crabs *Carcinus maenas* in an intertidal environment in relation to their morphology, prey availability and competition. *Marine Ecology Progress Series* 392: 143–155.

Professional journals and conference proceedings

- Van Noordwijk, C.G.E. and A. Klimkowska. 2013. Profiteren geleedpotigen van maaiselverspreiding in natuurontwikkelingsgebieden? *De Levende Natuur* 114:226–231.
- Versluijs, R., M. Geertsma, R. Felix, H. Turin and C.G.E. van Noordwijk. 2013. Eerste vondst van de blinde loopkever *Anillus caecus* in Nederland (Coleoptera: Carabidae). *Entomologische Berichten* 73:185–190.
- Versluijs, R., J.J. Vogels and C.G.E. van Noordwijk. 2013. Mierengemeenschappen in het heidelandschap. *De Levende Natuur* 114:220–225.
- Van Noordwijk, C.G.E. and M. Nijssen. 2012. Graslandbeheer bekeken door insectenogen. Stikstof en versnippering vragen om een nieuwe aanpak in kalkgraslanden. *Vakblad Natuur Bos en Landschap* 9:24–27.
- Peeters, T.M.J., I. Raemakers, J. Kuper, A. Ovaa and C.G.E. van Noordwijk. 2012. Steilwandjes bij Bemelen, een voor bijen onmisbaar onderdeel van het hellingschraallandcomplex. *Natuurhistorisch Maandblad* 101:164–169.
- Van Noordwijk, C.G.E. 2011. Using life-history analyses to improve restoration management. *Proceedings of the Netherlands Entomological Society Meeting* 22:75–86.
- Berg, M.P., C.G.E. van Noordwijk and A. Kruithof. 2011. De Brede pissebed *Porcellio dilatatus* komt nog vrijlevend voor in Nederland (Isopoda: Porcellionidae). *Nederlandse Faunistische Mededelingen* 35:45–51.
- Smits, N.A.C., R. Bobbink, A.T. Kuiters, C.G.E. van Noordwijk, J.H.J. Schaminée and W.C.E.P. Verberk. 2009. Sleutelfactoren en toekomstperspectief voor herstel van het Limburgse heuvelland. *De Levende Natuur* 110:111–115.
- Van Noordwijk, C.G.E. and T.M.J. Peeters. 2008. Muurhagedissen op de Bemelerberg: over het hoofd gezien of over het hek gezet? *Natuurhistorisch Maandblad*, 97:145–148.
- Van Noordwijk, C.G.E., P. Boer and W. Dekoninck. 2007. Comment les fourmis du Thier de Lanaye nous apprennent à gérer les pelouses calcaires Néerlandaises. *Echo des Réserves* 4:4–7.
- Boer, P., W. Dekoninck and C.G.E. van Noordwijk. 2006. De mierenfauna van enkele kalkgraslanden van Thier de Lanaye en de herontdekking van *Lasius distinguendus* in België. *Bulletin van de Entomologische Vereniging (België)* 142:115–122.

- Peeters, T.M.J. en C.G.E. van Noordwijk. 2006. De Vierbandgroefbij, een bijzondere vondst op de Bemelerberg. *Natuurhistorisch Maandblad* 95:186–189.
- Smits, N.A.C., C.G.E. van Noordwijk, R. Huiskes, R. Bobbink, J. Willems, H. Esselink, H. Siepel, A.T. Kuiters and J.H.J. Schaminée. 2006. Herstel van schrale hellinggraslanden in Zuid-Limburg. *Natuurhistorisch Maandblad* 95:181–185.
- Beltman, B. en C.G.E. van Noordwijk. 2004. Kleinschalig plaggen van trilveen. *De Levende Natuur* 105:130–133.
- Van Noordwijk, C.G.E. 2002. Water oak as a witness of climate change. *Eidos* 1:46–51.

Reports and websites

- Van Noordwijk, C.G.E., M.J. Weijters, N.A.C. Smits, R. Bobbink, A.T. Kuiters, E. Verbaarschot, R. Versluijs, J. Kuper, W. Floor-Zwart, H.P.J. Huiskes, E. Remke and H. Siepel. 2013. Uitbreiding en herstel van Zuid-Limburgse hellingschraallanden, Eindrapport 2^e fase O+BN onderzoek. Directie Agro kennis, Ministerie van Economische Zaken.
- Van Noordwijk, C.G.E., J.T. Kuper, W. Floor-Zwart, K. Alders, H. Turin, T. Heijerman, B. Aukema and H. Siepel. 2012. Knelpunten voor loopkevers, wantsen en sprinkhanen in hellingschraallanden. OBN rapport nr: OBN 2012-162-HE.
- Van Noordwijk, C.G.E., N.A.C. Smits, J.A. Weinreich, B. van Tooren, M. Nijssen and R. Bobbink. 2012. Heuvelland. Pages 16–42 in: Jansen, A.J.M., H.F. van Dobben, D. Bal and N.A.C. Smits. *Herstelstrategieën stikstofgevoelige habitats, Ecologische onderbouwing van de Programmatische Aanpak Stikstof (PAS), Deel III Landschapsecologische inbedding van de herstelstrategieën*. Alterra Wageningen UR and Programmadirectie Natura 2000, Ministerie van Economische zaken, Landbouw en Innovatie.
- De Hullu, E., J. Vogels, C.G.E. van Noordwijk, R. Bobbink and B. van Tooren. 2011. Herstelstrategie hellingschraallanden. In: De Hullu, E. and J. Vogels. *Herstelstrategieën voor Nederlandse ecosystemen op basis van Landschapsprocessen: Een verkenning*. Bargerveen rapport.
- Van Noordwijk, C.G.E., R. Loeb and R. Bobbink. 2010. Vooronderzoek Eyscherheide, vegetatie, bodem en fauna. Stichting Bargerveen rapport 2010.11.
- Smits, N.A.C., C.G.E. van Noordwijk, R. Bobbink, H. Esselink, R. Huiskes, A.T. Kuiters, W.A. Ozinga, J.H.J. Schaminée, H. Siepel, W.C.E.P. Verberk and J.H. Willems. 2009. Onderzoek naar de ecologische achteruitgang en het herstel van Zuid-Limburgse hellingschraallandschappen. Rapport DKI nr. 2009/dk118-O, Ministerie van Landbouw, Natuur en Voedselkwaliteit.
- Bobbink, R., R.J. Bijlsma, E. Brouwer, K. Eichhorn, R. Haveman, P. Hommel, C.G.E. van Noordwijk, J. Schaminée, W.C.E.P. Verberk, R. de Waal and M.F. Wallis de Vries. 2008. Preadvies hellingbossen in Zuid-Limburg. Rapport DK nr. 2008/094-O, Ede.
- R. Bobbink and C.G.E. van Noordwijk. 2007. Kalkgrasland, betekenis en kenschets. www.natuurkennis.nl, Natuurtypen / Droge schraalgraslanden (N11) / Droog schraalland (N11.01) / Kalkgrasland.

Oral presentations

- Van Noordwijk, C.G.E. 2014. Through Arthropod Eyes: Using life-cycle knowledge to improve conservation success. Conservation research and practice conference. Edge Hill University, 14 May 2014, Ormskirk, UK.
- Van Noordwijk, C.G.E. 2014. Through Arthropod Eyes: Using life-cycle knowledge to improve conservation success. Seminar at Edge Hill University, 17 March 2014, Ormskirk, UK.
- Van Noordwijk, C.G.E., L. Baeten, M.P. Berg, H. Siepel, E. Remke and D. Bonte. 2013. Effects of 17 years of calcareous grassland restoration on diversity patterns differ for eight taxonomic groups. INTECOL conference, 18–23 August 2013, London, UK.

- Van Noordwijk, C.G.E., M.J. Weijters, N.A.C. Smits and R. Bobbink. 2013. Uitbreiding van hellingschraalland op voormalige landbouwgrond. Veldwerkplaats, 18 juni 2013, Bemelen, the Netherlands.
- Van Klink, R. and C.G.E. van Noordwijk. 2012. Biodiversity research in space and time. Netherlands Annual Ecology Meeting, 8 February 2012, Lunteren, the Netherlands.
- Van Noordwijk, C.G.E., D. Bonte, M.P. Berg, E. Remke and H. Siepel. 2011. How do landscape properties and species life-history traits determine landscape connectedness? 12th conference of the European Ecological Federation, 28 September 2011, Avila, Spain.
- Van Noordwijk, C.G.E. 2011. Using species' life-history traits to design restoration measures for fragmented habitats. Ecological seminar, department of terrestrial ecology, Gent University, 25 Februari 2011, Gent, Belgium.
- Van Noordwijk, C.G.E. 2011. Using species' life-history traits to design restoration measures for fragmented habitats. Netherlands Annual Ecology Meeting, 9 February 2011, Lunteren, the Netherlands.
- Van Noordwijk, C.G.E. 2011. Using life-history analyses to improve management for chalk grassland insects. Ecological seminar, department of Community and Conservation Ecology, Groningen University, 11 January 2011, Groningen, the Netherlands.
- Van Noordwijk, C.G.E. 2010. Using life-history analyses to improve restoration management for chalk grassland insects. 22^e Nederlandse Entomologendag, 17 December 2010, Ede, the Netherlands.
- Van Noordwijk, C.G.E. 2009. Herstel van karakteristieke fauna van hellingschraallanden. Veldwerkplaats Beheer hellingschraalland en -kalkgrasland, 30 September 2009, Gulpen, the Netherlands.
- Van Noordwijk, C.G.E. 2009. Restoration of species-rich chalk grasslands. Annual Meeting of the Netherlands Ecological Research Network, 10 February 2009, Lunteren, the Netherlands.
- Van Noordwijk, C.G.E. and H. Esselink. 2005. Effects of the current management regime on the entomofauna of calcareous grasslands. 4th European Conference on Ecological Restoration, 12-18 September 2005, Zaragoza, Spain.

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Bijenwulf - European beewolf (*Philanthus triangulum*)
Photo: Aart Noordam



Vuurspringer - jumping spider (*Philaeus chrysops*)
Photo: Aart Noordam



Ruwe pissebed - common rough woodlouse (*Porcellio scaber*)
Photo: Theodoor Heijerman



Kijk naar het landschap door de ogen van een ongewerveld dier!

Instructies:

- 1) Knip deze pagina uit langs de stippellijn.
- 2) Plak de pagina op stevig papier.
- 3) Knip of snij de ogen uit langs de stippellijntjes.
- 4) Knip de maskers los van elkaar.
- 5) Bevestig elastiekjes aan de zwarte rondjes.
- 6) Haak de elastiekjes om je oren en bekijk de wereld door de ogen van een ongewerveld dier.
- 7) Staan je ogen niet ver genoeg uit elkaar voor een Ruwe pisseped? Geen vier ogen aan de voorkant van je hoofd? De wereld bekijken door de ogen van ongewervelden is niet makkelijk!

Try looking at the landscape through arthropod eyes!

Instructions:

- 1) Cut page on dotted line.
- 2) Glue on thin cardboard.
- 3) Cut out eyes on dotted lines.
- 4) Separate the individual masks.
- 5) Tie rubber bands to the black circles.
- 6) Hook the bands behind you ears and see the world through arthropod eyes.
- 7) Are your eyes too close together for the Common rough woodlouse? Are you short on eyes for the jumping spider? It is not easy to observe the world through arthropod eyes!

Verschenen in de serie 'Mechanisms and constraints in biodiversity conservation and restoration':

1. Verberk, W.C.E.P. 2008. Matching species to a changing landscape – aquatic invertebrates in a heterogeneous landscape.
2. Remke, E. 2009. Impact of atmospheric deposition on lichen-rich, coastal dune grasslands.
3. Van Kleef, H.H. 2010. Identifying and crossing thresholds in managing moorland pool macroinvertebrates.
4. Vermonden, K. 2010. Key factors for biodiversity of urban water systems.
5. Van Turnhout, C.A.M. 2011. Birding for science and conservation. Explaining temporal changes in breeding bird diversity in the Netherlands.
6. Schipper, A.M. 2011. Multiple stressors in floodplain ecosystems. Influences of flooding, land use and metal contamination on biota.
7. Van Duinen, G.A. 2013. Rehabilitation of aquatic invertebrate communities in raised bog landscapes.
8. Van Noordwijk, C.G.E. 2014. Through arthropod eyes. Gaining mechanistic understanding of calcareous grassland diversity.

Het samenwerkingsverband tussen Natuurplaza en de Radboud Universiteit Nijmegen (IWWR) ontwikkelt, bundelt en verspreidt kennis op het gebied van herstel en behoud van biodiversiteit en ecosystemen.

In Natuurplaza participeren:

- Stichting Bargerveen
- Vereniging SOVON vogelonderzoek Nederland
- Stichting reptielen, amfibieën en vissenonderzoek Nederland (RAVON)
- Stichting floristisch onderzoek Nederland (FLORON)
- Zoogdiervereniging
- Vereniging onderzoek flora en fauna (VOFF)

Deze combinatie van organisaties verbindt het verspreidingsonderzoek met het wetenschappelijk onderzoek. De koppeling van veldwaarnemingen in ruimte en tijd met ecologische lab-, veld- en beheerexperimenten resulteert in innovatieve kennis. De Natuurplaza partners hebben een breed en actief netwerk van vrijwilligers. Hierdoor is er een continue vernieuwing, ontwikkeling en doorstroom van kennis, waardoor maatschappelijke vraagstukken snel en adequaat aangepakt kunnen worden.

Stichting Bargerveen heeft als doel het ontwikkelen van kennis voor systeemgericht natuurherstel met focus op fauna en het (inter)nationaal verspreiden van kennis. Daarnaast is het bijdragen aan de opleiding van studenten en junior onderzoekers een belangrijke doelstelling. De onderzoeksvragen die de stichting beantwoordt komen voort uit de problemen waar beheerders of beleidsmakers tegenaan lopen. Veel thema's zijn gerelateerd aan de effectiviteit van de beheersmaatregelen, alsmede aan de VER-thema's, zoals verzuring, vermesting en verdroging. Het onderzoek wordt uitgevoerd in binnen- en buitenland en in een scala van landschappen, waaronder de kustduinen, stuifzanden, kalkgraslanden, laagveenwateren, hoogvenen, heide en vennen.

Stichting Bargerveen is met de andere Natuurplaza partners gehuisvest binnen de Radboud Universiteit Nijmegen en werkt nauw samen met de afdelingen dierecologie en -ecofysiologie, milieukunde, aquatische ecologie en milieubiologie.



Stichting Bargerveen



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