

# Effects of large herbivores on grassland arthropod diversity

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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 141 studies on this topic of which 24 simultaneously investigated plant and arthropod diversity. Using the data from these 24 studies, we compared the responses of plant and arthropod diversity to an increase in grazing intensity. This quantitative assessment showed no overall significant effect of increasing grazing intensity on plant diversity, while arthropod diversity was generally negatively affected. To understand these negative effects, we explored the mechanisms by which large herbivores affect arthropod communities: direct effects, changes in vegetation structure, changes in plant community composition, changes in soil conditions, and cascading effects within the arthropod interaction web. We identify three main factors determining the effects of large herbivores on arthropod diversity: (i) unintentional predation and increased disturbance, (ii) decreases in total resource abundance for arthropods (biomass) and (iii) changes in plant diversity, vegetation structure and abiotic conditions. In general, heterogeneity in vegetation structure and abiotic conditions increases at intermediate grazing intensity, but declines at both low and high grazing intensity. We conclude that large herbivores can only increase arthropod diversity if they cause an increase in (a)biotic heterogeneity, and then only if this increase is large enough to compensate for the loss of total resource abundance and the increased mortality rate. This is expected to occur only at low herbivore densities or with spatio-temporal variation in herbivore densities. As we demonstrate that arthropod diversity is often more negatively affected by grazing than plant diversity, we strongly recommend considering the specific requirements of arthropods when applying grazing management and to include arthropods in monitoring schemes. Conservation strategies aiming at 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.

*Key words:* grazing, insects, invertebrates, plants, large grazers, ungulates, management, species richness, defoliation, soil compaction.

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## I. INTRODUCTION

Large grazing herbivores exert major influences on their habitat and are abundant and important in all grassland ecosystems (Hobbs, 1996; Olf, Ritchie & Prins, 2002). Populations and communities of large herbivores have been under human influence for millennia, with humans causing extinctions (Owensmith, 1989; Lorenzen *et al.*, 2011; Rule *et al.*, 2012) and changes in abundances (Owensmith, 1989). Additionally, ever since the first goats and sheep were domesticated over 11000 years ago (Zeder, 2008) agricultural livestock practices have intensified, culminating in the year 2000 in 26% of the terrestrial biome being used for livestock production as pasture or fodder crops (FAO, 2008). This may pose a threat to biodiversity through overgrazing (e.g. Smith, 1940), and habitat loss and fragmentation (e.g. Krueess & Tschardtke, 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 & Borner, 1995; Donlan *et al.*, 2006). It is therefore imperative to understand the influence of large grazing herbivores on the biodiversity of various plant and animal groups.

Effects of grazing on plant diversity are variable, with literature supporting both positive and negative effects

(Milchunas, Sala & Lauenroth, 1988; Olf & Ritchie, 1998). Reported effects on arthropod diversity are equally diverse, with studies reporting negative (e.g. Krueess & Tschardtke, 2002*a,b*; Pöyry *et al.*, 2004), positive (Joern, 2005; Woodcock & Pywell, 2009), or neutral (Bestelmeyer & Wiens, 2001; Hofmann & Mason, 2006) effects of large herbivores. Intuitively, a strong positive relationship between the diversity of resources (plants) and consumers (arthropods) would be expected (Murdoch, Peterson & Evans, 1972; Tilman, 1986), but evidence is mounting that the response of arthropod diversity to grazing deviates from that of plant diversity (e.g. Krueess & Tschardtke, 2002*a*; 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; Olf & Ritchie, 1998). Such a framework is largely missing for understanding effects of large herbivores on arthropod diversity (but see e.g. Morris, 2000; Bell, Wheeler & Cullen, 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 & Crossley, 1984).

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

vegetation properties) of large herbivores on arthropod communities. Finally, we synthesise these effects, discuss the implications for conservation of arthropod diversity and identify remaining questions.

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

## II. 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 (i) whether the response of arthropod diversity to grazing differs from that of plant diversity, and (ii) whether the response of arthropod diversity is related to the response of the plant community, ecosystem productivity or differences in experimental design among studies.

### (1) Literature search

We performed a systematic search (Pullin & 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-making or abandonment. Only studies meeting the following three criteria were assessed: (i) published or in press in international, peer-reviewed scientific journals in Thomson Reuters *Web of Science*, accessible to the University of Groningen; (ii) performed in (semi)-natural grass- or heathland ecosystems; (iii) with arthropods identified to species

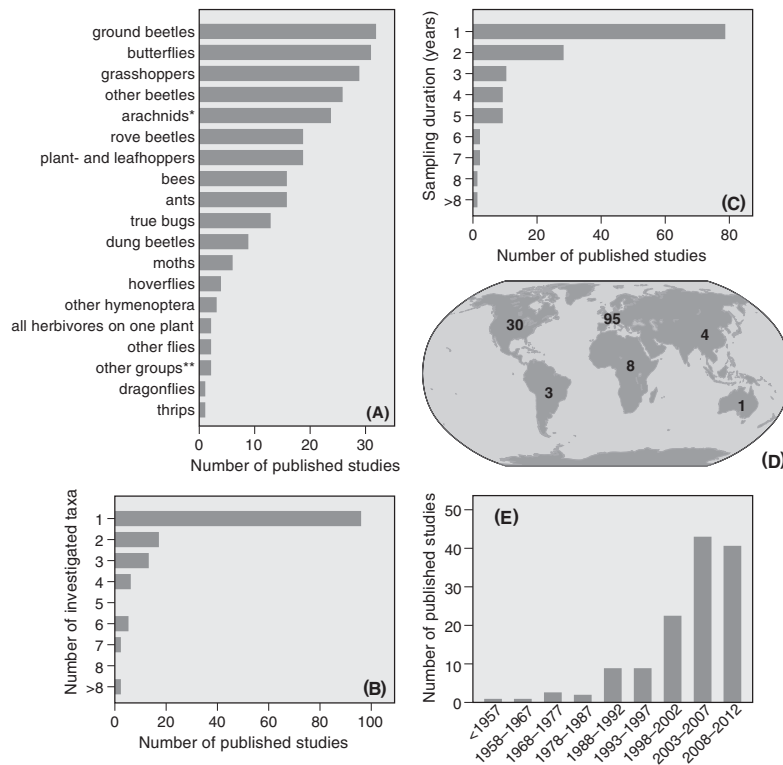
level. Studies in which grazing effects were potentially confounded with other variables (such as soil type or climate) were omitted. We initially used cross-referencing to get an overview of the groups of arthropods commonly assessed, and finally performed searches on each of these groups, as well using general search terms 'insects', 'arthropods' and 'invertebrates' (see online Table S1) in combination with 'graz\*' in *Web of Science*.

### (2) Dataset description

Our search yielded 141 studies assessing the effects of large herbivores on arthropod communities published between 1940 and May 2013, sometimes in combination with other management types (see online Table S1). An overview of the taxonomic and geographic focus of all 141 studies is given in Fig. 1. Ground beetles, butterflies and grasshoppers have been studied most extensively, while other, sometimes extremely species-rich groups, such as parasitic Hymenoptera, (non-syrphid) flies and aphids have received virtually no attention (Fig. 1A). More than half of the studies assessed only one taxonomic group, with less than 25% of studies assessing more than two arthropod taxa (Fig. 1B). The number of years that arthropods were sampled during these studies varied: in about half of the studies arthropods were sampled for only 1 year while only during two studies were data collected for 8 years or more (Fig. 1C).

The majority of grazing studies were conducted in Europe (>65%; Fig. 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 (see online Table S2). More than half of the studies were published after 2002 (Fig. 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.*, 1992a,b; Dennis *et al.*, 1997; Joern, 2005; Rickert *et al.*, 2012). These include studies using exclosures to exclude some or all vertebrate herbivores within sites (e.g. Morris, 1967; Fisher, Barham & Stewart, 2005; Gómez & González-Megías, 2007). The controlled experiments usually ran for less than 10 years (although some impressive examples of long-term experimental grazing research exist, see online Table S1) and had a relatively small number of replicates (maximum three). In the historical studies, effects of grazing were compared among a number of sites that differed historically in densities or species of herbivore (e.g. Smith, 1940; Kruess & Tscharrntke,



**Fig. 1.** Research focus of 141 published studies assessing the effects of large herbivores on arthropod diversity, conducted in open landscapes (grass- or heathlands) with arthropods identified to species level. (A) Studied taxa, (B) taxonomic spread (number of investigated taxa), (C) duration of sampling, (D) geographic location, and (E) year of publication (until 2012). We documented the identity of the most commonly assessed taxonomic groups (usually to order level, but sometimes to family or class level). A complete list of the analysed studies and definitions of arthropod groups can be found in Tables S1 and S3. \*Arachnids: spiders, harvestmen, pseudoscorpions; \*\*other groups: Mantodea, Phasmatodea, Neuroptera, Dermaptera.

2002*a,b*; Nickel & Hildebrandt, 2003). Here, the number of replicate sites and the geographical extent were usually larger, but the sites did not necessarily have a constant grazing pressure or identical starting conditions. In our database, experimental and historical studies were represented approximately equally.

### (3) Statistical analysis

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

plant diversity were obtained directly from the authors. For studies where plant or arthropod richness responses to grazing were only reported in graphs, we used *ImageJ* software (Abramoff, Magalhaes & Ram, 2004) to extract accurate estimates of richness.

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

included per study. When more than two grazing intensities were reported in a study, all pairwise comparisons were included as separate data points, as were multiple sites per study (whenever reported separately). This resulted in a total of 61 data points. A complete list of the analysed studies and definitions of arthropod groups can be found in Tables S1 and S3.

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 same response variable for arthropods described above and 'publication' was again used as a 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 & Ritchie, 1998; Proulx & Mazumder, 1998; Bakker *et al.*, 2006). Duration of treatment was included as the number of years since the most recent management change. Productivity and difference in grazing intensity between compared treatments were included as ordinal variables and estimated from the site descriptions (productivity: '1' for unproductive systems such as steppes and heathlands, '2' for mesotrophic grasslands and '3' for productive systems such as savannahs, floodplains and salt marshes; difference in grazing intensity: '1' indicates a small difference in herbivore density, for instance low *versus* moderate density, whereas '3' indicates a large difference in density e.g. ungrazed *versus* intensively grazed, '2' was used for intermediate differences). Interaction terms were not included, as there was no *a priori* biological reason to assume any of these to be of particular relevance. To obtain an estimate of the variation explained by this second model, we obtained a pseudo- $r^2$  using the recently published method for mixed models (Nakagawa & Schielzeth, 2013) using the MuMIn package for R (Barton, 2013). This gives the 'marginal  $r^2$ ', which represents the variance explained by the fixed factors, and the 'conditional  $r^2$ ', representing the variance of both the random and the fixed factors. All analyses were performed in R 2.14.1 (R Core Team, 2013), with use of the lme4 package (Bates, Maechler & Bolker, 2013).

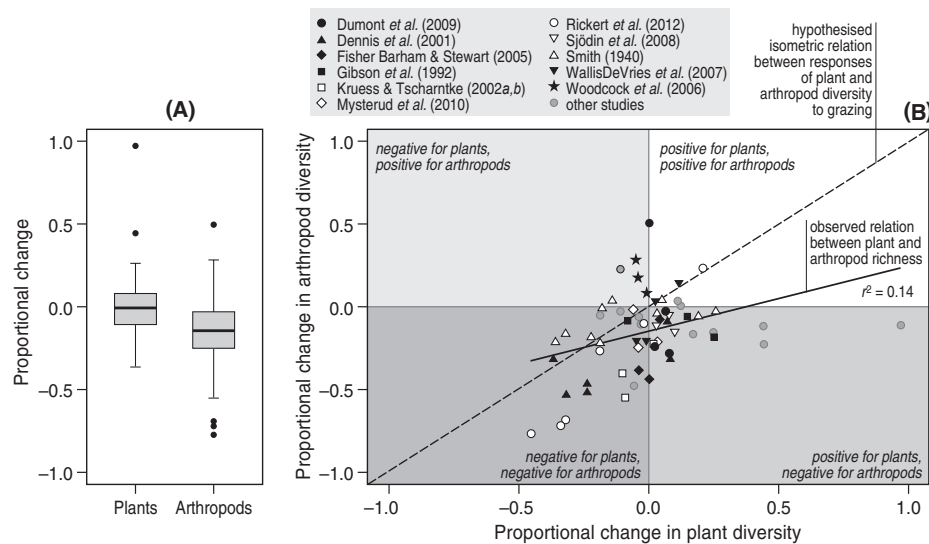
#### (4) Results

There was large variation in response of both plant and arthropod diversity to grazing (Fig. 2A). Across all studies, arthropod diversity responded significantly negatively to an increase in grazing intensity (GLMM:

$\mu = -0.14 \pm 0.04$ ,  $t = -3.36$ ,  $P = 0.002$ , Fig. 2A), with over 80% of the data points showing a decrease in richness. Plant diversity, however, did not show a significant response to grazing (GLMM:  $\mu = 0.04 \pm 0.04$ ,  $t = 0.98$ ,  $P = 0.33$ ), with approximately as many positive responses as negative ones (Fig. 2B). When the two effects were compared, the response of arthropod diversity was significantly more negative than that of plant diversity (GLMM:  $\mu = -0.15 \pm 0.03$ ,  $t = 4.54$ ,  $P < 0.001$ , Fig. 2A). The second mixed model, including multiple explanatory variables, revealed a significant, but weak positive relationship between the responses of plant and arthropod diversity to grazing ( $\beta = 0.41 \pm 0.13$ ,  $t = 3.28$ ,  $P = 0.004$ , model fit:  $\chi^2 = 9.65$ ,  $P = 0.002$ , Fig. 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 combined (conditional  $r^2$ ) explained 55% of the total variation, indicating large variation in response to grazing among studies.

### III. MECHANISMS UNDERLYING GRAZING EFFECTS ON ARTHROPOD DIVERSITY

The quantitative analysis in Section II showed that (i) the prevailing effect of large-herbivore grazing on arthropod diversity is negative, (ii) within studies, arthropod diversity responds more negatively to grazing than does plant diversity, (iii) the response of plant diversity to grazing is a poor predictor for the response of arthropod diversity, and (iv) 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).



**Fig. 2.** Comparison of the response ratios of plant and arthropod diversity to an increase in grazing intensity (median  $\pm$  interquartile range, whiskers represent  $1.5 \times$  interquartile range, dots represent outliers) (A) and the relationship between these response ratios (B) Data were extracted from 24 studies published between 1940 and 2013 reporting on the effects of grazing on both plant and arthropod diversity, supplemented with data obtained from several authors (see online Table S1).

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: (i) abiotic conditions of the environment (including non-trophic use of biotic structures), (ii) trophic resource availability and (iii) predation (Chase & Leibold, 2003). We use these determinants to classify the mechanisms by which arthropods are affected.

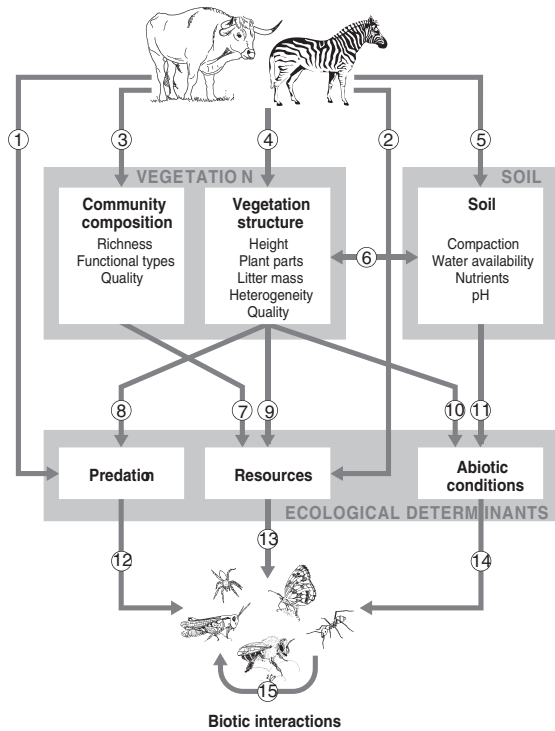
### (1) Direct effects

Large herbivores can affect arthropod diversity directly through unintentional ingestion or trampling (Fig. 3, Path 1), but also by supplying resources for specialised groups such as dung feeders and scavengers (Fig. 3, Path 2).

Large herbivores frequently ingest arthropods as a by-product of their forage intake. Such unintentional predation can lead to reduced arthropod population sizes (Bonal & Muñoz, 2007; Gómez & González-Megías, 2007; Van Noordwijk *et al.*, 2012b). The potential consequences at the community level have rarely been measured, but defoliation by mowing is known to cause high direct arthropod mortality (reviewed by Humbert, Ghazoul & Walter, 2009). Gómez & González-Megías (2007) demonstrated large differences between guilds of herbivorous insects in susceptibility to unintentional predation. While endophagous insects (living within

plant structures) often were ingested by large herbivores, ectophagous insects (living on plants) were generally not affected. Aphids and ladybirds, for example have been shown to avoid ingestion by dropping off the plant when detecting the breath of large vertebrates (Gish, Dafni & Inbar, 2010; Ben-Ari & Inbar, 2013). However, in short vegetation with limited possibilities to escape, and during immobile life stages (eggs and larvae) ectophagous species also may be ingested (Van Noordwijk *et al.*, 2012b). These differences in vulnerability to incidental ingestion among arthropod guilds suggest a large potential for shifts in arthropod communities.

Large herbivores also cause direct disturbance while moving through their habitats; most evident in the form of trampling living vegetation, litter and soil (Cumming & Cumming, 2003; Hobbs, 2006; Fig. 3, Path 1). Knowledge on the extent to which this affects arthropods is limited, but there is some observational (Chappell *et al.*, 1971; Bayfield, 1979; Bonte & Maes, 2008; Woodcock & Pywell, 2009) and experimental (Duffey, 1975) evidence that trampling by herbivores or humans mostly negatively affects population sizes and diversity of arthropods. It is not always clear, however, whether these effects resulted directly from direct trampling on arthropods, or indirectly, through changes in soil, litter or plant characteristics (see also Sections III.2 and III.3). Duffey (1975) demonstrated convincingly that even low frequencies of 5–10 treads per month on litterbags were highly detrimental to the arthropod fauna, and Chappell *et al.* (1971) showed large decreases in faunal abundance between lightly and heavily trampled calcareous



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

grasslands. For less-mobile arthropods, such as caterpillars, but also for large dung beetles (Negro, Rolando & Palestini, 2011) trampling could be an underestimated direct source of mortality (Fig. 3, Path 1). Additionally, frequent disturbance by large herbivores may decrease habitat suitability for arthropods. This may again be of greater importance for less-mobile species that could experience difficulties in returning to their host plants, like many larval insects (Dennis, Young & Gordon, 1998; Kruess & Tschardt, 2002a), and may even be evident at low herbivore density, when no measurable effect on vegetation characteristics is documented (Kruess & Tschardt, 2002b).

Conversely, large herbivores may have positive effects by directly supplying resources to arthropods in the form of dung, carcasses, blood and living tissue (Fig. 3, Path 2). Studies investigating the effect of dung on arthropod communities mostly focused on dung beetles, despite the fact that termites (Freyman *et al.*, 2008) and various fly families also feed on dung. Not surprisingly, these studies often report positive effects of large-herbivore presence on dung beetle diversity and abundance (Lumaret, Kadiri & Bertrand, 1992; Verdu *et al.*, 2007; Jay-Robert *et al.*, 2008), but high herbivore densities may be detrimental to dung beetle abundance and diversity (Jankielsohn, Scholtz & Louw, 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 & Strong, 1987; Madsen *et al.*, 1990) and dung decomposition rates (Wall & Strong, 1987; Beynon *et al.*, 2012).

Although it is intuitive that the presence of herbivores may enhance the diversity of scavenging and parasitic arthropods, field studies showing such patterns are scarce (Barton *et al.*, 2013). Evidence has been presented that a deer carcass can be a hotspot for biodiversity compared to the surrounding forest (Melis *et al.*, 2004) and that the presence of large herbivores can increase tick populations (Keesing *et al.*, 2013), but decrease populations of mice and their fleas (McCauley *et al.*, 2008). For these arthropod groups, human influence may be of extra importance, because in many grazed ecosystems, the resources that these species depend on are highly managed. For instance, removal of carcasses and treatment with anti-parasitic medication are very common in European semi-natural grasslands. Also targeted extermination of livestock parasites has large impacts on parasite populations. For example, the presence of cattle treated with acaricides reduces tick abundance (Keesing *et al.*, 2013), and several species of parasites have been eradicated from

parts of their former range (e.g. Wilson, 1986; Vreysen *et al.*, 2000). Nevertheless, introductions of livestock outside their native range have probably enhanced the spread of their parasites even more (e.g. Scholl, 1993). Anthropogenic causes of changes in large herbivore densities, with in its most dramatic form extinctions of species, will almost certainly lead to co-extinctions of their parasites (Dunn *et al.*, 2009) and scavengers.

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

## (2) Vegetation-structure-mediated effects

The most prominent effect caused by large herbivores is defoliation, leading to a decrease in vegetation height and structural complexity (Fig. 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 (Fig. 3, Path 3), which will be discussed in Section III.3. For arthropods, short and tall vegetation types provide different abiotic conditions, food resources and predation risk (Fig. 3, Paths 8–10). Currently emerging insights into how these differences affect arthropod diversity are outlined below.

The abiotic conditions arthropods are exposed to differ vastly between short and tall vegetation (Fig. 3, Path 10). When vegetation is permanently grazed short and bare soil is exposed, this often leads to a warmer microclimate in the vegetation and higher soil temperatures, which are essential for the larval development of various thermophilous arthropods such as many grasshopper and butterfly species (e.g. Thomas *et al.*, 1986; Cherrill & Brown, 1992; Bourn & Thomas, 2002; Roy & 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, Thomas & Sotherton, 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, Hambler & Brown, 1992*b*), for species that pupate (many parasitoid Hymenoptera) or deposit eggs (e.g. some grasshopper species) in or on plants, and offers hiding and stalking opportunities for predatory arthropods in the canopy (e.g. crab spiders, praying mantes).

Resource availability also differs between tall and short vegetation (Fig. 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 (Gómez, 2003) and insects developing in flowerheads and fruits (Morris, 1967, 1971*bb*; Völkl *et al.*, 1993; Gómez & 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 & Denno, 2004).

Conversely, short-grazed vegetation offers resources in the form of short-statured plants, that many specialised herbivorous insects depend upon (Thomas *et al.*, 1986; Van Klink *et al.*, 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 & 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 & Bazely, 1993; Nykanen & Koricheva, 2004). Specialist arthropods, however, have often co-evolved with their host plants in such a way that they tolerate or even profit from the secondary compounds that are produced after defoliation by large herbivores (Poelman *et al.*, 2009).

Furthermore, predation risk is modulated by vegetation height (Fig. 3, Path 8). Large-eyed predators, such as some ground beetle species (Morris, 2000), but also vertebrate predators, such as birds (Belovsky, Slade & Stockhoff, 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 & Denno, 2004).

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



& Lawlor, 1981). It is therefore likely that heterogeneous vegetation, consisting of a patchwork of short and tall vegetation will generally harbour the highest arthropod diversity.

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

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

To complicate matters, the effects of grazing on vegetation structure vary across spatial scales (WallisDeVries, Laca & Demment, 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 & 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.

### (3) Vegetation-community-mediated effects

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

Arthropod (consumer) diversity has been hypothesised to be correlated with plant (producer) diversity (Murdoch *et al.*, 1972; Tilman, 1986), and experimental increases of plant diversity have indeed been shown to increase arthropod diversity (Siemann *et al.*, 1998; Haddad *et al.*, 2009), abundance (Haddad *et al.*, 2001), functional group richness (Siemann *et al.*, 1998; Rzanny & Voigt, 2012) and food-web complexity (Scherber *et al.*, 2010; Rzanny & 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 & Tschardtke, 2002a; Pöyry *et al.*, 2004), and the generality of these results is corroborated by our quantitative review (Section II). The response of plant diversity to grazing therefore seems to be a poor predictor for the response of arthropod diversity.

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

small loss in diversity, while the gain of tall-statured species can potentially cause a large increase.

Another obvious way by which large herbivores modify the composition of plant communities is by changing the relative abundance of different plant functional groups (Fig. 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, Schimel & Holland, 1995). In temperate systems, both intensive grazing and cessation of grazing can cause an increase in the relative cover of grasses (McNaughton, 1986; Milchunas & Lauenroth, 1993). Consistent with these observations, species richness of polyphagous and grass-feeding insects was found to be highest under intensive grazing (Nickel & 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, Potts & Willmer, 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*.

#### (4) 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 & Lauenroth, 1993; Bakker, Olf & Gleichman, 2009) and increased soil compaction (Trimble & Mendel, 1995) (Fig. 3, Path 5). Changes in soil conditions can lead to changes in plant communities (Liddle, 1997) (Fig. 3, Path 6), but can potentially also have direct effects on aboveground arthropods (Fig. 3, Path 11).

Although the effects of grazing on belowground fauna are strong (Bardgett & 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 eggs or larvae. 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 & 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 & Mason, 2006) and some ant species (Bestelmeyer & Wiens, 2001). The generality of these effects is, however, as yet poorly known.

#### (5) Effects on interactions among arthropod species

Like all organisms, co-occurring arthropod species interact in myriad ways, including resource competition, predation and mutualistic interactions (Fig. 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 among 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 (Tschardtke, 1997). The general dearth of knowledge on the response of parasitoid Hymenoptera to habitat change (Shaw & Hochberg, 2001; Shaw, 2006), however, inhibits generalisation, and in fact positive effects of large herbivores on parasitoid abundance in experimental thistle patches have been reported (Vanbergen *et al.*, 2006).

There is, however, a great potential for bottom-up-driven diversity control in grasslands, as suggested by the strong relationship between vegetation complexity and arthropod diversity (Section III.2). An increase in abundance or diversity of herbivorous insects and detritivores can potentially increase the diversity of higher trophic levels, as was shown in plant diversity manipulation experiments (e.g. Scherber *et al.*, 2010). From grazing experiments, so far only correlative evidence is available, showing similar changes in the diversity of herbivorous and predatory taxa to changes in grazing pressure (Gibson *et al.*, 1992a; Kruess & Tschardtke, 2002b; Báldi, Batáry & Kleijn, 2013). Moreover, the diversity of parasitic Hymenoptera was found to correlate well with overall diversity (Anderson *et al.*, 2011), suggesting that these potentially respond indirectly to herbivore-mediated changes in diversity of lower trophic levels. Still, causal relations explaining these changes have not yet been mapped in the context of grazing.

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

Finally, it is possible that grazing alters competitive outcomes between arthropod species from the same trophic level. For plants, it is well established that grazing strongly alters competitive relationships (Hobbs & Huenneke, 1992; Olf & Ritchie, 1998), but

for arthropods, evidence is scarce. The importance of competitive exclusion in arthropod communities has been debated for decades (Lawton & 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 & Trumble, 2002; Kaplan & Denno, 2007), it remains unclear how important these processes are in structuring natural communities in a field setting. Since the vast majority of arthropod species exploit different resource bases, the importance of competition among species in limiting diversity is probably small (Strong *et al.*, 1984). Therefore, the disruption of competitive hierarchies by large herbivores is unlikely to have great impacts on arthropod diversity (Fuentes & Jaksic, 1988). Disentangling the relative importance of all these processes remains a formidable future challenge.

#### IV. SYNTHESIS

##### (1) Why is arthropod diversity so often negatively affected by grazing?

Ultimately, the mechanisms through which large herbivores affect arthropods are mediated by three key main components of arthropod population regulation: predation, trophic resource availability and abiotic conditions (Fig. 3). In the presence of large herbivores, (unintentional) predation and direct mortality of arthropods are likely to increase, which is especially likely to affect sedentary arthropods (Section III.1). These direct effects will be negative for diversity if mortality rates are high, but not detrimental if arthropod populations can be maintained.

The total trophic resource availability for arthropods will be reduced as herbivores consume plants and litter, which form the base of the arthropod food web (Section III.2). Therefore, overall arthropod abundance is likely to be reduced under grazing. Given the large body of theoretical (Fisher, Corbet & Williams, 1943) and empirical evidence (Kruess & Tscharntke, 2002a; Pöyry *et al.*, 2006) showing a positive relationship between abundance and diversity of organisms, defoliation by large herbivores can be expected to be negative for arthropod diversity. However, plant diversity is often increased by grazing (Olf & Ritchie, 1998), creating opportunities for a wider group of specialist herbivores (Section III.3). Also for species such as dung beetles and parasites resource abundance will increase with grazing (Section III.1).

Large herbivores often strongly modify the abiotic environment experienced by arthropods (Section III.2). Such modifications will be positive for some species and negative for others. Overall effects of changes in microclimatic conditions on diversity therefore depend

on the habitat requirements of the species present in the regional species pool and the interactions of large herbivores with prevailing (microclimatic) 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 (Section III). Therefore, arthropod diversity *can* be augmented by large herbivores if the following conditions are met: (i) grazing causes an increase in biotic and abiotic heterogeneity, (ii) 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 (iii) this positive effect of increased heterogeneity is large enough to compensate for the negative effects of direct mortality and resource competition between arthropods and large herbivores. This combination of conditions is most likely to occur at low densities of herbivores, because direct mortality and resource competition are minimal, while variation in (a)biotic conditions is most likely to increase (see Section III.2).

High densities of large herbivores are likely always to be detrimental to arthropod diversity, although some arthropod species or groups may profit. This is indeed supported by most empirical studies (e.g. Gibson *et al.*, 1992a; Kruess & Tscharntke, 2002a,b; Nickel & 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).

##### (2) Why is arthropod diversity affected more negatively by grazing than is plant diversity?

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

First, plant diversity is generally increased by grazing through a decrease in light competition and an increase in colonisation by new species (Olf & Ritchie, 1998). Since there is no evidence for an important role of competition in limiting arthropod diversity (Section III.5), it is unlikely that large herbivores can cause any type of competitive release on arthropod communities. Conversely, the majority of species at the base of the arthropod food web (herbivores and detritivores) compete directly for resources with large herbivores, as outlined in Section IV.1. This competition is highly asymmetrical, and can lead to competitive exclusion and decreased population sizes (Gómez & 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 & Thomas, 2002). Plants are sedentary

and need a specific set of conditions that are all met at one site. Arthropods generally have distinct phases in their life cycle, which often need different site conditions (e.g. warm microclimate and abundant host plants for larval development and nectar for adult life stages). In particular, during immature stages many species have a narrow niche and limited ability to actively find suitable habitat patches (Bourn & Thomas, 2002). For arthropods to survive, the requirements of all life-cycle stages must be met within the area an individual can travel. This means that single arthropod species often need a certain level of habitat heterogeneity (creating favourable microclimatic conditions and food resources for all life stages) at a specific spatial scale to survive. Plant species, on the contrary, can thrive in fairly homogeneous grasslands as long as their specific habitat requirements are met. As more intensive grazing management generally decreases habitat heterogeneity (see Section III.2) this is inevitably detrimental to many arthropod species, even if the requirements of individual life stages are still met. In addition, the life cycle of many arthropod species is strictly 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 & Lennartsson, 2010; Van Noordwijk *et al.*, 2012a)

Third, plants are more plastic in their response to grazing than are arthropods. 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.

### (3) Implications for arthropod conservation management

Most grassland types worldwide depend on the presence of large herbivores to prevent succession to scrub or forest (Hobbs & 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 (Mbanjo *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, Williams & Tang, 2008) and abundances (Hutchinson & King, 1980) of arthropods. Also, in natural and semi-natural grasslands, arthropods are not always given high priority, but awareness of the importance of arthropods is growing among conservationists, as is attention for arthropods in conservation and restoration research (Fig. 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 in 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 (Olf & Ritchie, 1998; Wilson *et al.*, 2012) and many thermophilous insects, including many butterflies depend on favourable microclimates (Bourn & Thomas, 2002) created by more intensive grazing (see Section III.2). Both plants and thermophilous butterflies characteristic of semi-natural grasslands have become severely threatened due to increased eutrophication and abandonment of traditional farming practices (Ostermann, 1998; Van Swaay *et al.*, 2010) and, hence, are of special conservation interest (Van Swaay *et al.*, 2010). This creates potential for conflict between the requirements of plant diversity, threatened arthropod species and maintenance of high overall arthropod diversity (see for example Negro *et al.*, 2013). In habitat restoration, where arthropod populations of high conservation value are absent, a focus on plant restoration in the first few years may be justified, as this is a prerequisite for the establishment of many arthropod species (Woodcock *et al.*, 2010, 2012). However, in a conservation context, solutions should be sought to meet the requirements of as many species as possible by conserving or promoting a heterogeneous habitat. Low densities of herbivores provide the best chance of attaining this objective (see Section IV.1), but so far no evidence has been presented that a single management regime can accommodate all species in a local species pool (Dennis *et al.*, 1997; Dennis, Young

& Bentley, 2001). Therefore, it has been suggested that arthropod diversity can best be conserved at the landscape scale by maintaining grasslands under different types of management in close proximity (Dennis *et al.*, 1997; Morris, 2000; Kruess & 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, Clarke & Rispin, 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, Scherber & Tschardtke, 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, van Noordwijk & Hildrew, 2013). This approach has been advocated for conservation purposes (Van Noordwijk *et al.*, 2012a), but can also be used actively to suppress populations of pest species (Onsager, 2000).

## V. NEXT STEPS

From this review, clear patterns explaining the patterns of arthropod diversity in grazed ecosystems have emerged. Analysing the mechanisms affecting arthropod diversity responses to grazing has revealed why generally arthropod diversity responds negatively to (intensive) grazing and how the variation in these responses can be explained. Our study has also identified a number of issues that remain poorly understood and require further research. Although we have argued that a positive effect of large herbivores on arthropod

diversity can mostly be expected at low herbivore densities, empirical evidence remains scarce, and more experimental testing is needed. In particular we need to expand our knowledge of the specific conditions under which large herbivores have a positive effect on arthropod diversity, for example by directly comparing a number of promising low-intensity grazing regimes. As we have demonstrated that spatial and temporal heterogeneity in (a)biotic conditions are crucial to arthropod diversity, these aspects need special attention. It has become apparent that there are large differences between arthropod taxa in their response to grazing. Therefore, multi-taxon studies are highly desirable, preferably conducted over multiple years to account for weather effects and population dynamics. In addition, a great deal can be learnt from smaller experimental studies targeting single mechanisms (e.g. incidental ingestion, effects of soil compaction or effects of plant diversity). To add to our current knowledge, these experiments should especially focus on effects of these mechanisms at the community level (the extent to which diversity and composition are affected). Helpful approaches in this respect include (i) trait-based approaches, demonstrating which traits determine to what extent arthropod species are affected by certain mechanisms and (ii) 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.

## VI. 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 lacking.

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

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

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

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

(6) Conservation strategies aiming at maximising heterogeneity, such as low-intensity grazing, maintenance of different types of management in close proximity, or rotational grazing regimes, are most likely to conserve or restore arthropod diversity.

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## IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Table S1.** Geographic location, ecosystem, arthropod taxa, experimental setup and duration of the studies used for Figs 1 and 2.

**Table S2.** Studies on effects of large herbivores on arthropod diversity in wood- and scrublands.

**Table S3.** Definitions of taxonomic groups.

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