Effects of herbivores on grassland plant diversity
Han Olff and Mark E. Ritchie

Maintaining plant diversity is a central goal in the management of biodiversity throughout the world. Herbivores are generally thought to alter plant diversity by their direct consumption of competitively dominant plant species and by effects on plant competition. Consequently, management of herbivores has become a crucial component in efforts to restore or maintain biodiversity, particularly in grasslands. However, other studies suggest that herbivores sometimes have weak or even negative effects on plant diversity. Two recent research developments suggest avenues for explaining these discrepancies. First, several field studies suggest that herbivores control plant diversity through mechanisms that influence local plant colonization and extinction dynamics. Second, recent findings on differences in effects between types of herbivores, types of habitat and spatial and temporal scales are leading to new theoretical work that may guide future syntheses.

Conflicting results
The effects of herbivores on plant species richness appear to depend on the type and abundance of herbivore species in a particular environment. These effects can be either positive or negative. For example, natural populations of large grazing mammals are reported to increase plant diversity. The same is found when domesticated large grazers are managed at low stocking rates on productive grasslands. However, high stocking rates can decrease diversity. Insect herbivores often have weak or negative effects, although outbreaks of specialist herbivores on dominant plant species can increase plant diversity. Intermediate-sized, digging herbivores, such as prairie dogs, rabbits, and pocket gophers, create extensive, intense but aggregated soil disturbances that increase plant diversity.

Another source of variation in herbivore effects on plant diversity arises from the spatial or temporal scales at which diversity is measured or affected. Herbivores can influence species richness at both the local scale (plant neighborhood) and the regional scale (spatial range of an individual or population of herbivores). For example, local disturbances and selective grazing can enhance diversity at local scales, but strong selection for grazing-tolerant plant species within the species pool might reduce diversity at larger scales. In addition, herbivore body size might interact with the scale of diversity, because local effects of large herbivores can occur over a much larger spatial scale than local effects of smaller herbivores. The temporal scale of herbivore effects might also be important, because short-term increases in plant diversity from herbivore activity may ultimately disappear owing to herbivory-induced succession to a few defended or tolerant plant species. Alternatively, periodic outbreaks of smaller herbivores at intervals that are not detectable in short experimental studies could maintain high plant diversity. These results suggest that the spatial and temporal scale of herbivore effects must be explicitly considered to explain their impact on plant species richness.

The effects of herbivores on plant diversity also differ with the environment. Grazing mammals in more productive grasslands, such as temperate grasslands in Europe or tall grasslands in the western Serengeti, increase plant diversity. Grazers in arid or very saline environments often do not change or can even decrease diversity. For example, herbivores in North American tallgrass prairie on poor soils decrease plant diversity, whereas those on rich soils increase it.

New approaches
Recent developments suggest new ways to explain these conflicting results. First, plant species richness is increasingly thought to result from the balance between local colonization and extinction rates of species, and the mechanisms that influence these rates. Second, there is increasing recognition that herbivore body size could explain the direction, magnitude and scale of herbivore effects on plant species richness. Finally, recent studies link herbivore dynamics and diversity to plant community dynamics across environmental gradients. This work provides a new conceptual framework that allows us to predict herbivore effects as a function of the supply of plant resources.

A spatial concept of plant species richness
Early research on determinants of species richness in grasslands focused on mechanisms enhancing resource partitioning and coexistence of plant species. These mechanisms included spatial variation in resource availability and limitation of plants by different resources. However, other research has stressed that local species richness is determined by local colonization and regeneration processes, which are governed by the number of species available to colonize the area from a species pool at larger spatial scales.
Both ideas are merging into a new synthesis. Within this, it is proposed that local species richness in grasslands is maintained by a dynamic interaction between local colonization (via dispersal and establishment) from species pools at larger spatial scales and local extinction (e.g. because of competitive exclusion). This synthesis is inspired by island biogeography theory. As a result, high plant diversity should occur when local extinction rates of species (relative to the number of species present) are lower than local colonization rates. This suggests that processes determining grassland diversity can be classified into two groups: (1) processes contributing to enhanced local colonization rates, and (2) processes contributing to reduced local extinction rates (Table 1). The extensive literature suggests that herbivores influence grassland plant diversity through any or all of these mechanisms (Table 1, Figs 2 and 3).

**Colonization processes and extinction-related processes** (e.g. resource competition) are not mutually exclusive. Reduction of dominant competitors by herbivore grazing can enhance the persistence of plant species that colonize the disturbed areas generated by herbivores. Thus, the interaction of the two processes could further strengthen herbivore effects on grassland diversity. The ultimate effect of herbivores on plant diversity might, therefore, depend on their relative impacts on the biomass and reproduction of dominant plant species, the density and type of regeneration sites and the supply of propagules from rare plants.

### Importance of herbivore type and scale

Differences in the effects among different herbivore and environment types remain largely unexplained, even in extensive reviews of the subject. However, insight is emerging into the relationships between herbivore body size, variation in their digestive capability, spatial scale of effect and vulnerability to predators. Small nondigging herbivores, such as insects and small mammals, generally create relatively few soil and plant canopy disturbances and do not often reduce the biomass of tall, coarse, competitively dominant grassland plants. In short experimental studies,

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**Table 1. Overview of major processes determining local plant species richness in grasslands, and proposed effects of herbivores on those processes**

<table>
<thead>
<tr>
<th>Mechanism increasing diversity</th>
<th>Main direction (^a)</th>
<th>Effects of herbivores</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local colonization processes</td>
<td>Enhanced propagule dispersal through soil on hooves, seeds attached to fur, feathers, exoskeletons, etc., and through dung or faeces deposition</td>
<td>Competitive interactions between plants are relaxed by herbivore consumption</td>
</tr>
<tr>
<td>Higher input of propagules of new species to a site</td>
<td>Removal of seeds and reproductive structures</td>
<td>Preferential consumption of competitively dominant plants</td>
</tr>
<tr>
<td>Higher availability of propagules of extant species</td>
<td>Disrupts grasses by digging mammals or trampling creates gaps, generating high light, nutrient-rich and pathogen-free soil</td>
<td>Plants shift from competing for light to competing for soil nutrients, which allows more functionally different plant species to coexist, especially when attended by some spatial heterogeneity in nutrient supply rates</td>
</tr>
<tr>
<td>Availability of regeneration niches allowing establishment</td>
<td>Soil disturbances stimulate germination from the soil seed bank</td>
<td>Tall species lose more biomass and become more nutrient limited than palatable species</td>
</tr>
<tr>
<td>Local extinction, competitive exclusion processes</td>
<td>The positive effect of increased water and nutrient availability in gaps can be counterbalanced by unfavorable thermal conditions that increase soil evaporation and plant transpiration</td>
<td>Less competition for limiting resources</td>
</tr>
<tr>
<td>Less competition for limiting resources</td>
<td>Enhanced propagule dispersal through soil on hooves, seeds attached to fur, feathers, exoskeletons, etc., and through dung or faeces deposition</td>
<td>Competitive interactions between plants are relaxed by herbivore consumption</td>
</tr>
<tr>
<td>Different species are limited by different nutrients</td>
<td>Removal of seeds and reproductive structures</td>
<td>Preferential consumption of competitively dominant plants</td>
</tr>
<tr>
<td>More spatial and temporal variation in resource supply</td>
<td>Disrupts grasses by digging mammals or trampling creates gaps, generating high light, nutrient-rich and pathogen-free soil</td>
<td>Plants shift from competing for light to competing for soil nutrients, which allows more functionally different plant species to coexist, especially when attended by some spatial heterogeneity in nutrient supply rates</td>
</tr>
<tr>
<td>Spatial and temporal variation in rates of biomass loss (disturbance) in which intermediate levels of disturbance prevent competitive dominance by the local resource competitors but do not create environments too extreme for rare species</td>
<td>Soil disturbances stimulate germination from the soil seed bank</td>
<td>Tall species lose more biomass and become more nutrient limited than palatable species</td>
</tr>
</tbody>
</table>

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\(^a\) Indicates whether diversity is generally enhanced (+) or decreased (−) through herbivore effects upon each process.
they might, therefore, have weak or even negative effects on plant diversity. In years of peak abundance, however, they can heavily defoliate dominant plant species and increase diversity26. Intermediate-sized herbivores (1-5 kg), such as herbivorous birds25 and digging mammals, can reduce the biomass of dominant species under certain conditions1,9. However, digging by mammoths of this size to escape predators can create soil disturbances that enhance plant colonization and establishment and thus increase local diversity27. Furthermore, a high preference to forage in the vicinity of cover (such as shrubs) to avoid predators28 could enhance existing spatial variation in vegetation structure and enhance diversity at larger spatial scales.

Large grazing herbivores, such as livestock and ungulates, however, have more consistent effects. They can produce abundant low-quality food (i.e. competitively dominant grassland plants)19,33 and typically create frequent, small disturbances across the landscape29. Larger herbivores may be more efficient seed dispersers than smaller ones by transporting soil and undamaged seeds over larger distances. Their spatially heterogeneous urine deposition could also increase regeneration sites and soil heterogeneity29. Thus, larger herbivores increase plant diversity through many different mechanisms. However, large herbivores at high density, such as in intensive livestock grazing, can graze unsuitably and/or create widespread erosive, detrimental soil disturbances, leaving only a few tolerant plant species, thus reducing plant diversity29. Herbivore effects on plant diversity can therefore shift from weak and intermittent effects to strong effects across a continuum of small to large herbivores. However, the direction of effects (either positive or negative) could depend as much on environmental characteristics as on the type of herbivore.

**Effects across environmental gradients**

Results of herbivore enclosure experiments in different types of grassland suggest that the effects of herbivores vary predictably across environmental gradients. The characteristics of herbivores and plants, expected in different environments, could influence how herbivores affect plant diversity (Fig. 4). Recent work22,36–41 couples plant-resource interactions, plant competitive dynamics and herbivore population dynamics and suggests that soil fertility gradients and precipitation gradients could be crucial to explain patterns in herbivore effects on plant diversity (Table 2). Ratios of the supply of different plant resources determine productivity and the tissue characteristics of competitively dominant plant species. Tissue characteristics can influence the palatability of dominants and thus whether herbivores will mediate plant extinction rates by preventing competitive exclusion. For example, ungulates, productive environments feature intense light competition and thus have greater potential for herbivores to increase local colonization rates of plant species.

Grassland environments naturally classify into four major habitat types (Table 2). Dry environments on infertile soils have low productivity and favor plants that compete well for both nutrients and water in the absence of herbivory (e.g. in deserts). Dominant species can either be ephemeral or have water retention mechanisms operating through light reflection or transpiration reduction (via thorns, hairs, wax layers, woody structures and secondary chemicals) that also deter herbivory29. Such a plant community may, therefore, support a few, small herbivores, and these herbivores are likely to select rare, palatable species. Hence, they will have little effect on plant competition and consequently induce few plant extinctions through mechanisms. Therefore, herbivory could increase extinction rates. Because of the low productivity and already extensive bare soil in these environments, herbivores...
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may have little effect on colonization rates by opening the plant canopy. Low natural abundance of herbivores implies that few plants in the species pool have evolved a tolerance to grazing. Introductions of high densities of large mammalian grazers that were supplementary fed, such as live-stock, are therefore likely to reduce diversity dramatically.

In dry environments on fertile soils, competitively dominant plant species tend to be palatable and support high densities of many herbivore species (e.g. in East African savannas). These plant species are likely to tolerate, rather than avoid, herbivory because of the good regrowth opportunities. High nutrient availability in fertile soils could have weak positive effects on diversity because only a few plants that are intolerant to grazing remain in the species pool to colonize ungrazed areas.

On infertile soils with nonlimiting precipitation (e.g. in chalk grasslands, heathlands or unfertilized meadows), dominant plants are likely to have low tissue nutrient concentrations but to be sufficiently productive to induce light competition. These plants will probably only be used by large grazers, which can tolerate low plant tissue quality. Grazing, therefore, might shift competition (locally) from light to soil nutrients, allowing more species to coexist. Such effects facilitate smaller herbivores, which increase extinction rates of rarer nondominant species but balance this local extinction by enhancing the regeneration of these species through soil disturbance. Thus, herbivores, especially large grazers, could dramatically increase diversity in these environments.

On fertile soils with nonlimiting precipitation (e.g. in agricultural pastures, salt marshes or river flood-plains), dominant plants are productive and light competition is important in the absence of grazing. Strong light competitors (such as tall grasses and woody plants), which dominate these habitats in the absence of grazers, are likely to be unpalatable (because of the high stem:leaf ratios) to all but the large herbivores when mature. Grazing by large herbivores opens the canopy, so that a few grazing-tolerant plant species replace the tall species. These tolerant species, which are able to regrow quickly after being grazed, support high densities of grazers, which impose acceptably high mortality rates on species that are less tolerant to grazing. Facilitation by large herbivores may create opportunities for small, selective herbivores (e.g. insects and small mammals) that may further reduce plant diversity because they prefer rare, palatable species.

Conclusion

Recent work on herbivore mediation of plant diversity has shifted the question from ‘do herbivores have an effect?’ to ‘why do effects differ?’ Herbivores appear to affect plant diversity through their impact on dominant plant species, plant regeneration opportunities and propagule transport. The strength of their effects range from weak to strong across a continuum from small to large herbivores. Furthermore, these effects depend on regional variation in major habitat characteristics, such as soil fertility and water availability, which determine herbivore abundance and the number of plant species that have evolved herbivore avoidance or tolerance strategies. These generalizations may lead to more understanding of why similar herbivores positively influence diversity in some environments but not others. They may also help to understand more of the magnitude

![Fig. 4. Shifting effects of herbivores on plant diversity across an environmental gradient. Cattle grazing for 15 years in the tidal salt marsh on the island of Schiermonnikoog, The Netherlands, increased plant diversity on low salinity soils but decreased it on high salinity soils. Plant communities on low salinity soils (the high salt marshes) are sufficiently productive for plants to compete for light, so grazing by cattle is likely to prevent competitive exclusion of species that have small stature. Plants on high salinity soils are typically of small stature and are water-stressed. These stress factors may relax competitive interactions as resource supply rates exceed demands; thus, browsing reductions of dominant species (cows, grazing) may have little effect on colonization rates by opening the plant canopy. Low natural abundance of herbivores implies that few plants in the species pool have evolved a tolerance to grazing. Introductions of high densities of large mammalian grazers that were supplementary fed, such as live-stock, are therefore likely to reduce diversity dramatically.

![Table 2. Hypothesized effects of herbivory on grassland plant diversity in different grassland environments, taken from recent reviews and models of herbivore effects across environmental gradients.]

<table>
<thead>
<tr>
<th>Environment</th>
<th>Precipitation</th>
<th>Soil</th>
<th>Major limiting resource</th>
<th>Herbivore characteristics</th>
<th>Effects on plant diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Through extinction</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Large herbivores</td>
<td>Small herbivores</td>
</tr>
<tr>
<td>Dry</td>
<td>Fertile</td>
<td>Water</td>
<td>Nutrients</td>
<td>Rare, small</td>
<td>--</td>
</tr>
<tr>
<td>Dry</td>
<td>Infertile</td>
<td>Water</td>
<td>Nutrients</td>
<td>Absent, diverse</td>
<td>--</td>
</tr>
<tr>
<td>Wet</td>
<td>Fertile</td>
<td>Nutrients</td>
<td>Light</td>
<td>Intermediate abundant, large</td>
<td>+</td>
</tr>
<tr>
<td>Wet</td>
<td>Infertile</td>
<td>Light</td>
<td>Nutrients</td>
<td>Absent, diverse</td>
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</table>

- Resource competed for by grazed plants.
- *Herbivores can be rare, intermediately abundant or abundant, and herbivore community is dominated by small or large herbivores or both (diverse).
- "Key: " + diversity is increased because extinction is reduced; -- diversity is decreased because extinction rates are higher.
- "Key: " + diversity is increased because local colonization is enhanced; -- diversity is decreased because local colonization is reduced.
- "Key: " *A diverse herbivore assemblage depends on the presence of large herbivores to facilitate smaller herbivores – otherwise herbivores will be rare.

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and direction of the effects of different types of herbivores and the spatial and temporal scales at which they operate. Placing the results of individual studies in this framework should help define contexts for biodiversity management and help resolve management controversies that arise from comparing conflicting individual studies.

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