Effects of herbivores on grassland plant diversity

Han Olff and Mark E. Ritchie

The role of herbivores in controlling plant species richness is a critical issue in the conservation and management of grassland biodiversity. Numerous field experiments in grassland plant communities show that herbivores often, but not always, increase plant diversity. Recent work suggests that the mechanisms of those effects involve alteration of local colonization of species from regional species pools or local extinction of species, and recent syntheses and models suggest that herbivore effects on plant diversity should vary across environmental gradients of soil fertility and precipitation.

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Maintaining plant diversity is a central goal in the management of biodiversity throughout the world. Herbivores are generally thought to decrease plant species richness by their direct consumption of competitively dominant plant species and by increasing diversity at larger spatial scales (34). Consequently, management of herbivores has become a crucial component in efforts to restore or maintain biodiversity, particularly in grasslands (32). 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 (16). The same is found when domesticated large grazers are managed at low stocking rates on productive grasslands (3-5). However, other studies suggest that herbivores sometimes have weak or even negative effects on plant diversity. For example, herbivores in North American tallgrass prairie on poor soils decrease plant diversity (22), whereas those on rich soils increase it (23).

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 (32). However, other research has stressed that local species richness is determined by local colonization and regeneration processes (33), which are governed by the number of species available to colonize the area from a species pool at larger spatial scales (8).
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 low soil and plant canopy disturbances and do not often reduce the biomass of tall, coarse, competitively dominant grassland plants. In short experimental studies,

### 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>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local colonization processes</td>
<td>+</td>
<td>Enhanced propague dispersal through soil on hooves, seeds attached to fur, feathers, exoskeletons, etc., and through dung or faeces deposition</td>
<td>-Preferential consumption of competitively dominant plants</td>
</tr>
<tr>
<td>Higher input of propagules of new species to a site</td>
<td>+</td>
<td>Removal of seeds and reproductive structures</td>
<td>Competitive interactions between plants are released by herbivore consumption</td>
</tr>
<tr>
<td>Higher availability of propagules of extant species</td>
<td>-</td>
<td>Disruption of digging mammals or trampling creates gaps, generating high light, nutrient-rich and pathogen-free soil</td>
<td>Preferential grazing on patches with attractive plant species (especially when these are free of predators and enemies), creating spatial heterogeneity in attractive and unattractive plant species across landscapes</td>
</tr>
<tr>
<td>Availability of regeneration niches allowing establishment</td>
<td>+</td>
<td>Soil disturbances stimulate germination from the soil seed bank</td>
<td>Localized urine and faeces deposition, aggregated soil disturbances through digging, trampling paths and wallows, etc.</td>
</tr>
</tbody>
</table>

- $^a$ Indicates whether diversity is generally enhanced (+) or decreased (−) through herbivore effects upon each process.

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**Fig. 1.** Herbivore effects on plant diversity at different spatial scales. (a) Hypothetical species-area curves for grazed (dashed line) and ungrazed (solid line) communites in a case where herbivores enhance diversity at small scales by reducing plant competition and increasing regeneration sites but inhibit diversity at larger scales by selecting for a restricted plant species pool of grazing tolerant plants. (b) These theoretical predictions are supported by a study of cattle grazing in Argentinian pampa, in which plant diversity was greater in grazed (circles) than ungrazed (squares) treatments when small areas were compared, but was lower when samples from larger areas were compared. Diversity is measured as $H$, where $H$ is the Shannon–Wiener diversity index, which estimates effective species richness or the number of equally abundant species that would yield the same value as calculated for the actual plant community. Redrawn, with permission, from Ref. 24.

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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 diversity\cite{10}. Intermediate-sized herbivores (1–5 kg), such as herbivorous birds\cite{11} and digging mammals, can reduce the biomass of dominant species under certain conditions\cite{12}. However, digging by mammals of this size to escape predators can create soil disturbances that enhance plant coloniz-
ations across the landscape\cite{12}. 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 heterogeneity\cite{12}. Thus, larger her-
bivores increase plant diversity through many mechanisms. However, large herbivores at high density, such as in intensive livestock grazing, can graze unspecifically and/or create wide-
spread erosive, detrimental soil disturbances, leaving only a few tolerant plant species, thus reducing plant diversity\cite{13}. Herbivore effects on plant diversity can therefore shift from weak and intermittent effects to strong effects across a con-
tinuum of small to large herbivores. However, the direction of effects (either positive or negative) could depend as much on the environmental characteristics as on the type of herbivore.

**Effects across environmental gradients**

Results of herbivore exclosure 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 environ-
ments, could influence how herbivores affect plant diversity (Fig. 4). Recent work\cite{14,15,16,17} couples plant-resource interac-
tions, plant competitive dynamics and herbivore population dynamics and suggests that soil fertility gradients and precipi-
tation gradients could be crucial to explain patterns in herbi-
vore effects on plant diversity (Table 2). Ratios of the supply of different plant resources determine productivity and the tissue characteristics of competitively dominant plant spe-
cies. Tissue characteristics can influence the palatability of dominants and thus whether herbivores will mediate plant extinction rates by preventing competitive exclusion. For exam-
ple, ungrazed, productive environments feature intense light competition and thus have greater potential for herbi-
vores to increase local colonization rates of plant species.

Grassland environments naturally classify into four ma-
jor 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 herbivory\cite{18}. 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. Therefore, herbivory could in-
crease extinction rates. Because of the low productivity and already extensive bare soil in these environments, herbivores

**Fig. 1.** The effects of herbivores on plant species richness in terms of island bio-
graphy theory\cite{19}. (a) Hypothetical relationships of colonization rates (solid lines) and extinction rates (dashed lines) with the number of existing species in a com-
munity. Herbivores are typically expected to increase colonization rates (grazed versus ungrazed, solid curve) and decrease extinction rates (grazed versus ungrazed, dashed curve), thereby increasing plant species richness in grazed communities \( \left( C_0 \right) \) relative to ungrazed communities \( \left( C' \right) \). (b) Local colonization and extinction rates measured for 57 years in Kansas shortgrass prairie that has been either grazed or grazed by cattle. Curves represent regressions of the number of spa-
cies appearing (colonization, solid lines) or disappearing (extinction, dashed lines) in 1 m² plots versus the number of species in each plot the previous year. Regressions were not significant for colonization rates (hence the horizontal lines) but were for extinction rates (\( r^2 = 0.46 \)). These data illustrate that herbivores can increase extinction rates as well as colonization rates, thus producing no significant effect on plant diversity. Redrawn, with permission, from Ref. 16.
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 it offers. 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. 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.

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 of effects.
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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