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Published in:
Trends in Ecology and Evolution

DOI:
[10.1016/S0169-5347\(98\)01364-0](https://doi.org/10.1016/S0169-5347(98)01364-0)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1998

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Citation for published version (APA):
Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, 13(7), 261-265. [https://doi.org/10.1016/S0169-5347\(98\)01364-0](https://doi.org/10.1016/S0169-5347(98)01364-0)

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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 enhance plant diversity by their direct consumption of competitively dominant plant species and indirect effects on plant competition¹⁻⁵. Consequently, management of herbivores has become a crucial component in efforts to restore or maintain biodiversity, particularly in grasslands^{6,7}. 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 synthesis.

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 diversity¹⁻⁵. The same is found when domesticated large grazers are managed at low stocking rates on productive grasslands⁶⁻⁸, but high stocking rates can decrease diversity^{2,9}. Insect herbivores often have weak or negative effects^{10,11}, although outbreaks of specialist herbivores on dominant plant species can increase plant diversity^{11,12}. Intermediate-sized, digging herbivores, such as prairie dogs (*Cynomys* sp.), rabbits (*Oryctolagus cuniculus*) and pocket gophers (*Geomys* sp.), create extensive, intense but aggregated soil disturbances that increase plant diversity¹³.

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) (Fig. 1). 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 scales¹⁴⁻¹⁶. In addition, herbivore body size might interact with the scale of diversity¹⁷, because local effects of large herbivores can occur over a much

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 these 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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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 herbivory can ultimately disappear owing to herbivory-induced succession to a few defended or tolerant plant species^{18,19}. Alternatively, periodic outbreaks of smaller herbivores at intervals that are not detectable in short experimental studies could maintain high plant diversity^{11,20}. 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 environment². Grazing mammals in more productive grasslands, such as temperate grasslands in Europe⁶⁻⁸ or tall grasslands in the western Serengeti^{4,21}, increase

plant diversity. Grazers in arid or very saline environments often do not change or can even decrease diversity^{2,6,9}. For example, herbivores in North American tallgrass prairie on poor soils decrease plant diversity²², whereas those on rich soils increase it²³.

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 resources²⁴⁻²⁶. However, other research has stressed that local species richness is determined by local colonization and regeneration processes²⁷, which are governed by the number of species available to colonize the area from a species pool at larger spatial scales²⁸.

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 theory²⁹. 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^{5,18,21} (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^{3,18,30}. 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,

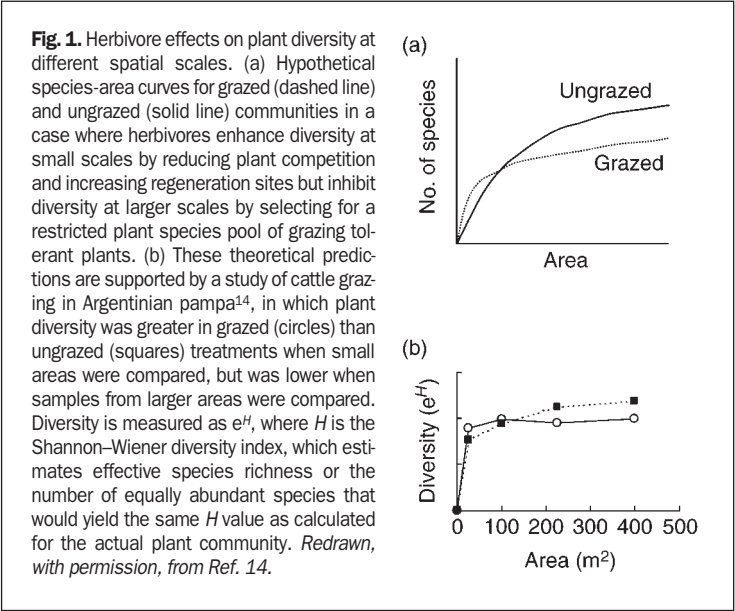


Table 1. Overview of major processes determining local plant species richness in grasslands, and proposed effects of herbivores on those processes

Mechanism increasing diversity	Effects of herbivores	
	Main direction ^b	Examples
Local colonization processes		
Higher input of propagules of new species to a site	+	Enhanced propagule dispersal through soil on hooves, seeds attached to fur, feathers, exoskeletons, etc., and through dung or faeces deposition
Higher availability of propagules of extant species	–	Removal of seeds and reproductive structures
Availability of regeneration niches allowing establishment	+	Disturbances by digging mammals or trampling creates gaps, generating high light, nutrient-rich and pathogen-free soil Soil disturbances stimulate germination from the soil seed bank
	–	The positive effect of increased water and nutrient availability in gaps can be counterbalanced by unfavorable thermal conditions that increase soil evaporation and plant evapotranspiration
Local extinction, competitive exclusion processes		
Less competition for limiting resources	+	Competitive interactions between plants are relaxed by herbivore consumption Preferential consumption of competitively dominant plants
Different species are limited by different nutrients	+	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 Tall species lose more biomass and become more nutrient limited than prostrate species
More spatial and temporal variation in resource supply	+	Localized urine and faeces deposition, aggregated soil disturbances through digging, trampling paths and wallows, etc.
Spatial and temporal variation in rates of biomass loss (disturbance) in which intermediate levels of disturbance prevent competitive dominance by the best resource competitors but do not create environments too extreme for rarer species	+	Selective 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
	–	High grazing pressure may result in dominance of only a few tolerant species
	–	Preferential grazing on rare, high-quality plant species (such as forbs)

^aCompiled from Refs 16, 25, 26 and 46–50.
^bIndicates 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 diversity²⁰. Intermediate-sized herbivores (1–5 kg), such as herbivorous birds³¹ and digging mammals, can reduce the biomass of dominant species under certain conditions^{13,30}. However, digging by mammals of this size to escape predators can create soil disturbances that enhance plant colonization and establishment and thus increase local diversity¹³. Furthermore, a high preference to forage in the vicinity of cover (such as shrubs) to avoid predators³² 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 use abundant low-quality food (i.e. competitively dominant grassland plants)^{19,33} and typically create frequent, small disturbances across the landscape³⁴. 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 heterogeneity³⁵. Thus, larger herbivores increase plant diversity through many mechanisms. However, large herbivores at high density, such as in intensive livestock grazing, can graze unselectively and/or create widespread erosive, detrimental soil disturbances, leaving only a few tolerant plant species, thus reducing plant diversity². 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 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 environments, could influence how herbivores affect plant diversity (Fig. 4). Recent work^{22,36–41} 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, ungrazed, 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 herbivory³⁶. 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 coexistence mechanisms. Therefore, herbivory could increase extinction rates. Because of the low productivity and already extensive bare soil in these environments, herbivores

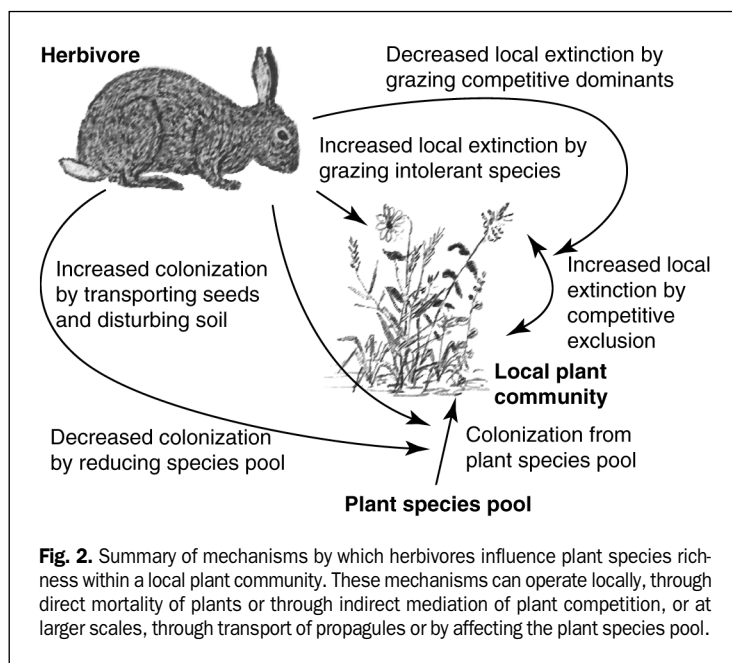


Fig. 2. Summary of mechanisms by which herbivores influence plant species richness within a local plant community. These mechanisms can operate locally, through direct mortality of plants or through indirect mediation of plant competition, or at larger scales, through transport of propagules or by affecting the plant species pool.

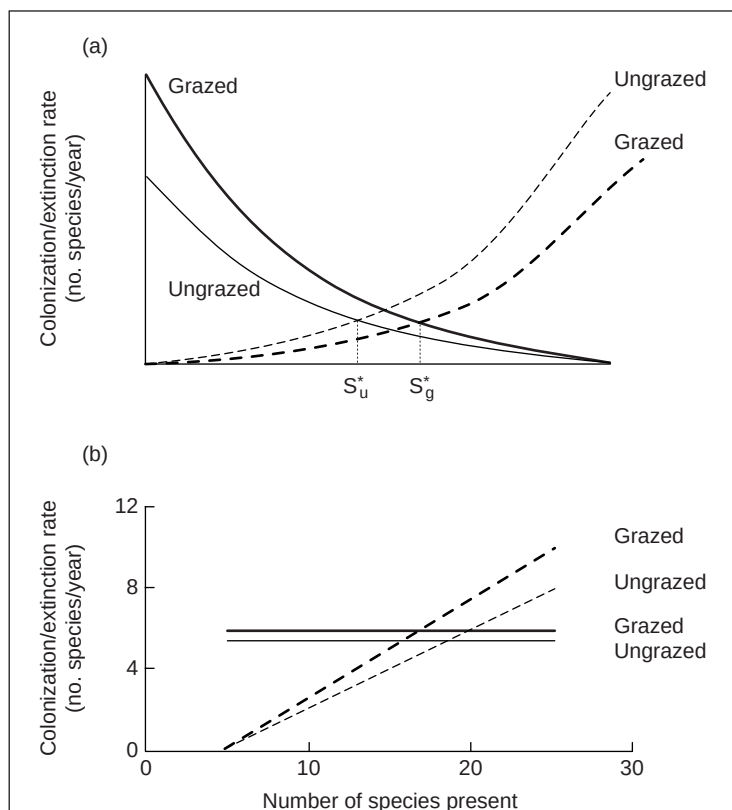


Fig. 3. The effects of herbivores on plant species richness in terms of island biogeography theory²⁹. (a) Hypothetical relationships of colonization rates (solid lines) and extinction rates (dashed lines) with the number of existing species in a community. Herbivores are typically expected to increase colonization rates (grazed versus ungrazed, solid curve) and decrease extinction rates (grazed versus ungrazed, dashed curve), thereby increasing plant species richness in grazed communities (S_g^*) relative to ungrazed communities (S_u^*). (b) Local colonization and extinction rates measured for 18 years in Kansas shortgrass prairie that has been either ungrazed or grazed by cattle¹⁶. Curves represent regressions of the number of species 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 yielding 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 herbivores² 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 livestock, are therefore likely to reduce diversity dramatically.

In dry environments on fertile soils, competitively dominant plant species tend to be palatable⁴² and support high densities of many herbivore species (e.g. in East African savannas)^{40,43,44}. These plant species are likely to tolerate, rather than avoid, herbivory because of the good regrowth opportunities owing to the high nutrient availability in fertile soils^{1,19}. In this case, exclusion of herbivores 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.

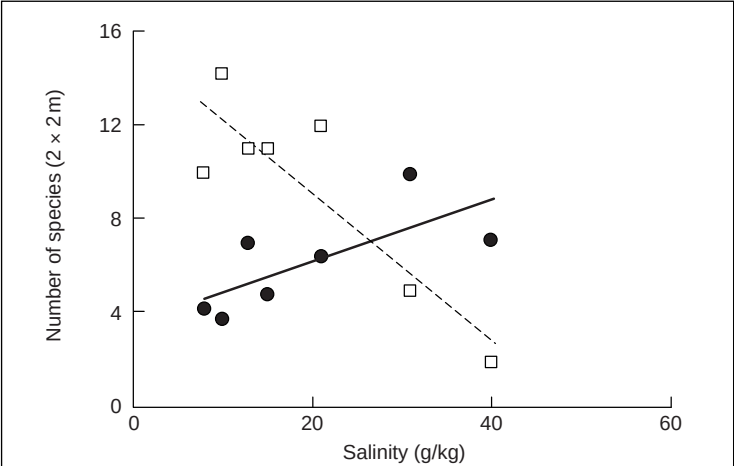


Fig. 4. Shifting effects of herbivores on plant diversity across an environmental gradient. Cattle grazing for 15 years in the tidal salt marsh on the island of Schiermonnikoog, The Netherlands, increased plant diversity on low salinity soils but decreased it on high salinity soils⁶. Plant communities on low salinity soils (the high salt marsh) are sufficiently productive for plants to compete for light, so grazing by cattle is likely to prevent competitive exclusion of species that have small stature³¹. Plants on high salinity soils are typically of small stature and are water-stressed. These stress factors may relax competitive interactions^{31,42} as resource supply rates exceed demands; thus, biomass reductions of dominant species have little consequences for subordinate species. Salinity stress also improves forage quality by preventing ‘dilution’ of nitrogen in plant biomass⁴², causing plants in saline parts of the salt marsh to be heavily fed upon. This may cause excessive damage to certain species, which reduces diversity. Soil compaction of wet (saline) soils and trampling by large herbivores can also inhibit plant diversity. Squares indicate grazed by cattle; circles, ungrazed. Data from Ref. 6.

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 competition³³. These plants will probably only be used by large grazers, which can tolerate low plant tissue quality⁴⁵. 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 unacceptably 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

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^{22,31,38,41}

Environment		Major limiting resource ^a	Herbivore characteristics ^b	Effects on plant diversity				Net effects
				Through extinction ^c		Through colonization ^d		
				Large herbivores	Small herbivores	Large herbivores	Small herbivores	
Precipitation	Soil							
Dry	Infertile	Water/nutrients	Rare, small	--	-	-	+	0/-
Dry	Fertile	Water	Abundant, diverse ^e	--	--	+	+	-
Wet	Infertile	Nutrients, light	Intermediately abundant, large	++	-	+	+	++
Wet	Fertile	Light	Abundant, diverse ⁵	+	-	+	+	+/-

^aResource competed for by ungrazed plants.
^bHerbivores can be rare, intermediately abundant or abundant, and herbivore community is dominated by small or large herbivores or both (diverse).
^cKey: +, diversity is increased because extinction is reduced; -, diversity is decreased because extinction rates are higher.
^dKey: +, diversity is increased because local colonization is enhanced; -, diversity is decreased because local colonization is reduced.
^eA diverse herbivore assemblage depends on the presence of large herbivores to facilitate smaller herbivores – otherwise herbivores will be rare.

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.

Acknowledgements

We thank Jan Bakker, Jan Bokdam, Wim Braakhekke, Hans de Kroon, Herbert Prins and Ruben Smit for useful comments on an earlier draft and discussion on the subject. We are also grateful to Maurits Gleichman for ideas and drawing the rabbit in Fig. 2. An anonymous referee made helpful suggestions on an earlier draft.

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