### Vertebrate Herbivory and Its Ecosystem Consequences

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Herbivory is a process where animals obtain energy and nutrients from vegetative plant parts (leaves, stems, etc.). Herbivory is called grazing, browsing or folivory, depending on the size of the herbivore and the type of plant tissue consumed. The consumption is actually performed by microbes in the digestive system. The role of the animal is to prepare the material and to provide a good environment for the microbes. This requires specializations, making herbivores a distinct animal group. This article focuses on consequences of herbivory by vertebrates. Vertebrate herbivory can change forests to heathlands or grasslands and influence the composition and species richness of the herbaceous vegetation.

# Introduction: Herbivory and the Landscape around Us

For residents of western and southern Europe, Middle East or Central Asia, there is no need to travel far to see the consequences of long-lasting, intense herbivory. When a UK citizen thinks about the nature of his/her home island, he is likely to think about the grasslands of South Downs or about the vast heathlands of Wales, northern England and Scotland. However, almost all these areas used to be covered by broad-leaved deciduous forests. On the European continent, current mountain nature is characterized by wide areas, with scattered trees in the middle of open meadows and heaths (Figure 1), indicating that the habitat would potentially be covered by forest. The Mediterranean region is currently largely occupied by low scrublands with their characteristic aroma. However, a few millennia ago, a large part of the region was covered by coniferous forest. Even the barren mountains of Central Asia used to have similar belts of coniferous forest between the arid steppedesert landscapes and the alpine zone as currently seen on

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#### Introductory article

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the mountains of the North American Great Basin (Walter, 1968).

Direct human actions have contributed to these changes, but all classical geobotanical texts (Ellenberg, 1988; Gimingham, 1972; Tansley, 1939; Walter, 1964) emphasize that these dramatic large-scale habitat changes were primarily due to the action of three initially native Eurasian herbivores - cattle, sheep and goats - which humans started to herd and protect against predators during the Neolithic Stone Age. Deforestation has also occurred in rugged mountain landscapes from where timber could never have been transported, indicating that long lasting browsing and the consequents failure of forest regeneration can cause deforestation even in the absence of logging. Moreover, reforestation of the treeless heaths and grasslands thus generated normally requires that the area is no longer used as a rangeland. Moreover, scattered trees and woodland patches occur in places where a lumberman could easily access but which are not attractive to herbivorous mammals. Sometimes, there is no external reason whatsoever for the presence of a tree in a given spot – some seedlings have just been lucky and reached safe size without being browsed (Figure 1). In his treatise of Central European plant geography, Ellenberg (1988) pointed out that trees mitigate the impacts of harsh climate, helping tree saplings to establish in the vicinity of adult trees already present. Therefore, all purely climate-dependent timberlines should be characterized by abrupt boundaries between closed forest and open country (tundra, alpine sward or steppe). When we see scattered trees on heaths or grasslands, we see evidence of herbivory.

The North American experience is very different. There, large-scale grazing systems were primarily established on



Figure 1 Tall, scattered trees in subalpine (upper panel, from French Alps) and subarctic (lower panel, from northern Norway) landscapes, shaped out by centuries of intense herbivory by cattle, sheep and goats (upper panel) or reindeer (lower panel). Photos were taken by Lauri and Tarja Oksanen.

natural grasslands or grass-shrub steppes. Instead of leading to the elimination of shrubs and woodland patches, domesticated herbivores have frequently triggered their expansion, the most (in)famous example being the invasion of the mesquite (*Prosopis* spp.) to the rangelands of the southwestern United States (Walter, 1968). These apparent contradictions will be clarified later.

#### Grazers, Browsers and Folivores

The capacity to exploit the abundant vascular plants belongs to the great innovations of animal evolution. This innovation has happened in only a few mammalian taxa, leading to the evolution of ruminants, horses, hares, elephants, hyraxes and a few groups of herbivorous marsupials (Kurtén, 1971). Also in the insect world, most herbivores belong to a few higher taxa (lepidopterans; i.e. butterflies and moths, sawflies, chrysomelid beetles and grasshoppers) which radiated extensively after this evolutionary breakthrough. In reptiles and birds, the situation is similar: the majority of higher taxa consist of predators, insectivores, fruit eaters and seed eaters.

To become a true herbivore, an animal must cross a seemingly impenetrable barrier, the cellulose-rich cell walls, enclosing all more digestible materials and all amino acids in the leaves and stems of vascular plants. This requires the right enzyme – cellulace – which animals cannot produce. All herbivores have solved this problem in the same way by having a large digestive system, which harbours cellulace-producing microbes. The role of herbivores themselves is to prepare the material, to maintain an environment favourable for the microbes and to absorb the products.

The cost of this breakthrough is that the animal has extra weight to carry when trying to escape a predator. Different herbivore groups have solved this problem in different ways. Most herbivorous mammals and grasshoppers have powerful legs, compensating for the extra weight. They rely on their speed and are sensitive to the slightest indication of predation risk. Thus, each of them has its 'landscape of fear', where habitats are ranked in accordance with their riskiness (Brown, 1999). Running with full speed, these herbivores outrun most predators; the big risk is to be taken by surprise. Therefore covered habitat means risk and open habitat means safety. Most rodents are slower than their predators and seek safety in underground cavities or treetops. For them, open habitats are normally more risky than habitats with cover. The contours of this 'landscape of fear' depend on experience. If predators remain absent, herbivores will change their behaviour and base their habitat choice on food quality. A single close call sharpens the contours of the landscape of fear, leading to radical changes in the habitat use. This has been seen after the reintroduction of wolves to Yellowstone National Park. Wolves have reduced herbivory pressure in risky habitats and increased the survival rates of tree seedlings much more rapidly than could be explained without considering the behavioural aspects of the interaction (Fortin et al., 2005).

In plants, herbivory selects for tolerance and/or resilience. Graminoids (grasses and sedges) have narrow leaves, growing from basal intercalary meristems. They can thus tolerate herbivory and grow rapidly after grazing as their meristems are practically inaccessible. Moreover, many graminoids accumulate silica in their leaves, making them hard to chew. As a countermeasure, herbivores have evolved continuously growing molars with lots of sharp ridges. Most woody plants and many herbaceous dicotyledons accumulate tannins and other phenol-based substances, which react with amino acids, making them unavailable for herbivores. Chewing woody plants requires different kinds of teeth than grinding graminoid leaves. Handling tannins requires high pH in the digestive tract, as high pH prevents tannins from reacting with amino acids. The trade-offs outlined above have resulted in a dichotomy between grazers, adapted to grind graminoids, and browsers, adapted to deal with the defences of dicotyledonous plants.

This dichotomy explains the seemingly contradictory experiences of domesticated grazers obtained in Eurasia and North America. In Eurasia, large-scale grazing systems have been run by indigenous peoples, who know that herds must contain both browsers and grazers to ensure the persistence of the system. In North America and East Africa, Europeans came as colonists and have often maximized their short-term profits by having only grazers, triggering an expansion of the least palatable shrubs and trees (Walter, 1964, 1968). Modern Eurasians face similar risks of mismanagement. In southern Norway, where the traditional grazing system with mixed livestock has been replaced by large-scale sheep ranching, the coarsest grasses have started to expand. Ranching single species thus amounts courting with disaster, unless the species is a generalist.

The term 'grazers' fits to some large and mobile invertebrates, such as grasshoppers and snails, but most herbivorous insects which sit and eat for a long time on the same food plant are referred to as folivores. This term is used, for example, for lepidopterans and sawflies. As compared with herbivorous mammals and grasshoppers, the possibilities of folivores to escape predators are limited. Their primary strategy is thus to grow as fast as possible so that the time spent in the vulnerable larval stage is minimized. The fitness of folivores thus depends on their growth rate, largely determined by the chemistry of the host plant, especially by the content of easily digestible nitrogen and defence substances. Some defensive compounds (e.g. tannins) influence the digestibility of the plant material (see above), others are acutely toxic. However, many folivores have evolved countermeasures, such as detoxification or sequestration, petiole cutting and leaf trenching. What is poison for one species can thus be optimal food for another. This evolutionary race between plants and folivores has played a central role in the evolution of folivorous insects. As the impact of these specialists is likely to be density-dependent, it has probably contributed to the high number of coexisting tree species in tropical rain forests.

Most folivore populations seem to be stable or fluctuate at low densities, but some species have dramatic outbreaks when they consume most available plant biomass. An example of such outbreak species is the autumnal moth, *Epirrita autumnata*, which periodically devastates hundreds of square kilometres of the mountain birch forest in northern Fennoscandia (Kallio and Lehtonen, 1975; Tenow, 1972). If folivores were not regulated by some density-dependent factors, the nature of our planet would probably look very different.

#### Herbivory and Mineral Nutrients

In the example of Great Britain, outlined in the introduction, we discussed the grasslands of South Downs and the heathlands of western and northern Great Britain. Both are products of long-lasting, intense grazing, but they look very different. Moreover, in many parts of western Europe, heathlands have been recently invaded by grasses. A likely underlying reason is the impact of mineral nutrients on the marginal costs of plant defences (Oksanen, 1990). Tannins and other phenolics, with which ericoids (heather like low, evergreen woody plants) defend themselves, are pure carbohydrates. If shortage of nitrogen or any other mineral nutrient limits the growth of a plant, it will accumulate reduced carbon, which can be used, for example, for tannin production at low costs. Conversely, in nutrient-rich habitats, allocations of reduced carbon atoms to tannins is done at the expense of growth, making the marginal costs of such defences high. Under such conditions, it is more advantageous for plants to be resilient, that is, to tolerate herbivory and to grow rapidly. Ericoids are thus favoured by the combination of intense herbivory and shortage of mineral nutrients. If nutrient supply increases, for example, due to airborne pollution, heathlands can be converted to grasslands (Roem and Berendse, 2000).

However, the relationship between mineral nutrients and the heathland-grassland issue is not a one-way street. In habitats with intermediate nutrient supply, grazing itself can tilt the balance to the favour of graminoids or ericoids (Olofsson et al., 2001). Selective nibbling with constant intensity normally favours ericoids (Bråthen et al., 2007), whereas variation between devastatingly intense herbivory and no herbivory at all is more likely to favour graminoids. As graminoid litter decomposes rapidly while ericoid litter is slow to decompose, ericoid dominance reduces the pool of available nutrients, whereas graminoid dominance increases it. These changes in the vegetation thus create positive feedback loops, which may result in alternative stable states. In the Arctic, this contrast is re-enforced by the cooling impact of dwarf shrub, litter, moss and humus layers on the soil, which slows down microbial processes. When grazers remove this cover, soils get warmer and nutrients are mineralized more rapidly (Zimov et al., 1995; Olofsson et al., 2004a). An example is seen along reindeer fences, where one side is periodically intensely grazed, whereas the other side is not (Figure 2).

#### Herbivory and Biodiversity

Many grazing-dependent European grasslands and heathlands are characterized by a high number of co-occurring plants and folivorous insects specialized on them. Cessation of grazing has often lead to dramatic reduction in biodiversity. Good examples are seen in the Baltic region, where the low-lying coasts and the limestone flats of the big islands have been intensely grazed since the Neolithic Stone Age. As long as intense grazing persisted, the coasts were fringed by species-rich meadows. Now, most of them have become reed monocultures (Siira, 1985). On the limestone flats, intense grazing created alvars - species-rich communities, dominated by prostrate plants. Even these unique and species-rich communities have been under the onslaught of invading tallgrasses and shrubs until increasing environmental awareness has lead to restoration of the grazing systems vital for their persistence (Rosén, 1982). The bottom line here is that reduction of herbivory leads to intensified competition for light, and competition for a single limiting resource tends to create monocultures (Grime, 1973). To prevent this from happening, herbivory need not be selectively directed to potential dominants. It is enough that the potential dominants are sensitive to herbivory, as typical for tall plants with erect shoots.

However, herbivory can also reduce species richness. Constantly intense herbivory creates an indirect interaction referred to as apparent competition (Holt, 1977) where plants support a shared consumer, which reacts positively to the increase of any of its resources. The ground rule of



Figure 2 The contrast between summer range, subjected to periodically intense reindeer grazing in late summer (right) and lightly grazed autumn range (left) on the mountains of northern Norway mountains. The fence across which the picture is taken is 40 years old. Photos were taken by Lauri and Tarja Oksanen.

apparent competition is that the species with the highest ratio of growth rate to loss rate wins. Whether this is a tolerant and rapidly growing grass or a relatively unpalatable ericoid species with low loss rate depends on the nutrient supply and type of grazing (see above), but there is no a priori reason to assume that apparent competition creates more species-rich communities than resource competition.

It has frequently been observed that the highest plant diversity is found in areas with intermediate grazing pressure – strong enough to prevent the tallest forb or grass species from outcompeting all other plant species but not so strong that a single species would consistently have the highest ratio of growth rate to loss rate (Grime, 1973; Connell, 1978). At intermediate levels of herbivory, the vegetation is often a mosaic of recently grazed patches and patches that have not been grazed for a long time. This temporal and spatial heterogeneity facilitates the coexistence of strong competitors and grazing tolerant or resistant plants at the landscape scale.

The rule described above is vague as the meaning of the word 'intermediate' is not specified. Indeed, many factors are involved. In the most unproductive habitats, highest species richness might be found at very low intensities of grazing, as plant growth is slow anyway and there are several potentially limiting resources, mitigating the impacts of competition on species richness. On oceanic islands, without native herbivorous mammals, highest richness of native species is normally obtained without any mammalian herbivory, as the native flora consists entirely of grazing-sensitive species. Grazing is maximally likely to have positive effects on the species richness in moist and nutrient-rich habitats, especially if these habitats lie in a region with many grazing-adapted plants in the species pool. However, treating species pool as an independent variable is problematic, because all species are products of natural selection and the survival of the fittest. It is therefore puzzling to find high numbers of grazing-adapted species in potentially forest-supporting boreal, moist-temperate and Mediterranean climates, where the persistence of open landscapes today depends on domesticated herbivores. However, in the not-so-distant evolutionary past, a diverse megaherbivore fauna roamed in the entire Palaearctic region, probably reducing the extent of closed forests in the same way as megaherbivores do today in East and South Africa.

At any rate, the interaction between herbivory and species diversity is complex, multifactorial and scale dependent. In a local scale, herbivores can increase species richness but the same herbivores can simultaneously reduce species richness in another habitat by favouring a vegetatively reproducing species with a high ratio of growth rate to loss rate. If, however, the last-mentioned species is grazingdependent, the maintenance of these habitats with low local species diversity can contribute positively to regional species diversity. An example of these complexities is provided by Fennoscandian mountain vegetation, where we found that grazing by reindeer could entirely change the composition of the vegetation (Figure 3). On these mountain meadows, local species richness is slightly higher in habitats where reindeer have been absent for 40 years (left panel), but red-listed plants are more frequent in the intensely grazed area (right panel), and occurrence of red-listed plants is positively correlated to the intensity of reindeer grazing (Olofsson and Oksanen, 2005).

#### Natural Regulation of Herbivory

Given the potential impact of herbivory on terrestrial vegetation, it is reasonable to wonder how there can be so many 'green worlds' - communities where plant biomass abounds and tall trees prevail - especially in areas outside Eurasia but even in the northern parts of Eurasia, where long-lasting winters have limited the development of largescale grazing systems. We have already seen that in spite of their mighty stature, trees are nothing but invulnerable to herbivores. Tall trees have large amounts of heterotrophic tissue (phloem, cambium and wood parenchyma) in their stems and roots, which must be fed by the canopy. Recurrent defoliation by folivorous insects results therefore in starvation and death. Moreover, trees start as seedlings and saplings and have two weak points. One is the phloem, which carries sugars from leaves to roots and is right under the bark. Many small mammals use phloem as winter forage, and a single ring of gnawed bark kills the sapling (Hansson, 1985). The other weakness is the leader shoot, which produces the hormones regulating the growth of lateral branches. Leader shoots are the most nutritious part of tree saplings and are therefore subject to maximally intense browsing. If the leader is browsed, lateral branches become secondary leaders and are now attracting browsers. Recurrent browsing thus tends to produce 'bonsais', which never reach safe size and are better forage than their non-browsed conspecifics (Chouinard and Filion, 2005; Welch et al., 1991). As long as the densities of browsers are moderate, such recurrently browsed bonsai saplings are just curiosities – but what prevents the numbers of browsers from increasing?

There are two contesting answers to the question what regulates the densities of herbivores and the intensity of herbivory in terrestrial nature: plant defences (Murdoch, 1966) and predation (Hairston et al., 1960). Plant defences are indeed important in determining what herbivores can eat and are likely to influence the growth rates of herbivore populations, but the tremendous impact of domesticated herbivores, discussed above, argues against the sufficiency of this mechanism. A counterargument is that many domesticated herbivores are today supplemented by proteinrich high-quality forage, grown in cropfields. However, this is only true for affluent countries and does not apply to areas where grazing and browsing really count. Even in Europe, the practices of food supplementation are recent. A few generations ago, when food was in short supply everywhere, no one would have come to the bizarre idea of growing protein-rich fodder plants in cropfields. In areas



Figure 3 Two variants of moist and nutrient-rich low alpine meadow. The left panel shows an area abandoned 40 years ago when the border fence of the legal summer range was constructed; the right panel is taken from the intensely grazed summer range. Photos were taken by Lauri and Tarja Oksanen.

with strongly seasonal climate, herds were moved seasonally along altitudinal gradients or winter forage was harvested by mowing semi-natural meadows and by coppicing native trees. However, the harvested forage was not especially nutritious but just allowed cattle and sheep, unable to cope with snow cover to survive the winter bottleneck.

In the recent past, more evidence for the pivotal role of predation has emerged. Predators have turned out to have tremendous impact on the steppe-forest boundary in the western United States (Ripple and Beschta, 2003, 2006). On predator-free land bridge islands, herbivores have wrecked havoc in tropical forests (Terborgh et al., 2006, 2001). We have contributed to these lines of evidence by introducing gray-sided voles to isolated islands in a big tundra lake, Iešjávri, in northernmost Norway. In this landscape, moist and nutrient-rich sites support dense thickets of gray willows in mainland areas (Figure 4, left panel), where predators are present, and on small, isolated islands, without either voles or predators. When gray-sided voles were introduced to these islands, the woody vegetation became devastated and largely replaced by tolerant herbaceous plants (Figure 4, right panel). The least palatable woody plants were actually best off in the *presence* of predators, as herbivory was then selective (Aunapuu *et al.*, 2008; Estes, 2009).

## Natural Herbivory in Arctic, Alpine and Arid Regions

There is a seemingly puzzling discrepancy between the strong impact of the reindeer on the Fennoscandian mountain and tundra vegetation (Figure 4, see also Bråthen *et al.*, 2007; Olofsson *et al.*, 2001) and the low density of the reindeer stock. The densities of reindeer, accounting to these dramatic impacts, range from one to five heads per square kilometre, that is, from 0.5 to 2.5 kg per ha, which is comparable to the biomass of microtine rodents on the tundra – and next to nothing, as compared to herbivore biomasses in most man-managed grazing systems at lower latitudes. The enigma is solved when we realize that the meadows depicted in Figure 4 melt out in late June or early July and are again snow covered by mid-September. The average July



**Figure 4** The vegetation of a moist and nutrient-rich low Arctic willow scrubland in the mainland (left) and of an initially similar habitat on an isolated island, where gray-sided voles were introduced in 1991 (right; photo taken in July 2008). Photos were taken by Lauri and Tarja Oksanen.

temperature is well below  $+10^{\circ}$ C, and blizzards can occur at any time. Although the herbaceous vegetation of nongrazed, moist and nutrient-rich tundra sites (Figure 4) may look lush, its annual primary production is severely limited by the low temperatures and the shortness of the growing season.

Rather than being consequences of high herbivore densities, the typically strong impacts of herbivorous mammals on Arctic-alpine vegetation are due to low growth rate of plants in these harsh environments, creating a situation where even relatively sparse herbivore populations can exert a strong impact on the vegetation (Oksanen et al., 1981; Oksanen and Oksanen, 2000). In such landscapes, predators cannot do much, because the densities of herbivores can be simultaneously too high to be sustainable for the vegetation and too low to yield predators a positive energy balance. As most of this impact is exerted during the long winters, it easily escapes the notion of the inexperienced, but comparison between mainland tundra areas and offshore islands and reindeer-free mountains, with wrapped in thick lichen carpets or copious moss banks (Dahl, 1957; Virtanen et al., 1997), demonstrate the tremendous impacts of herbivorous mammals in the Arctic (Crête, 1999; Crête and Doucet, 1998; Eskelinen, 2007; Hansen et al., 2007; Oksanen et al., 2008; Olofsson et al., 2004b; Tihomirov, 1959; Turchin et al., 2000; Virtanen, 1998, 2000; Virtanen et al., 1997).

Correspondingly, unproductive areas are also found on high mountains and in arid regions. We see them as variants on the same theme, but the details are determined by the specific features of each system. In alpine areas, winters are mild and snowy. Consequently, the ground freezes only little if at all (Dahl, 1957). This favours marmots and other hibernating mammals, which are absent from the Arctic. Moreover, the high winds and periodically warm days allow harvesting of winter forage, and options used by the pikas. Alpine ungulates can take advantage of the relatively short distances and follow the spring to the summits. All these features increase the importance of summer herbivory in alpine areas.

In arid regions, distances between productive and unproductive areas vary but even long distances can be covered quickly as the hard ground is favourable for rapid movements. It is thus easy to imagine how the herds of wild horses and cattle moved in these regions, exploiting spatial and temporal differences in plant growth. However, the arid regions were also the cradle of the domestication process. Therefore, the dominating herbivores of steppes and semideserts have for millennia been domesticated. If not extinct, the wild ancestors have been long ago reduced to tiny remnant populations without much impact on the vegetation.

Although the details differ, the heathland–grassland theme discussed in previous sections applies to Arctic, alpine and arid regions, too. Wherever we go in these unproductive areas, we find grasslands in nutrient-rich habitats, heathlands in a broad sense – low scrublands dominated by plants with high concentrations of secondary chemicals – in nutrient-poor ones (Walter, 1968). The interaction between herbivory and nutrient supply is thus basically similar, regardless whether the high herbivory pressure is due to high stocking rates or low primary productivity.

### Integrating Herbivory and Physical Environment

The traditional approach in explaining global patterns in herbivory has been to consider the climate as the independent variable, determining the characteristics of the vegetation, which, in turn, supposedly determines the intensity of herbivory and the characteristics of the herbivore guild. We have argued for a different approach – to start from food web dynamics and to treat the characteristics of the vegetation as consequences rather than causes of herbivore - plant dynamics, although we have also considered the interaction between herbivory and the supply of mineral nutrients. Note, however, that even we regard the climate as the ultimate independent variable. The difference as compared to the traditional approach lies in the pathway. We emphasize the indirect pathway where climate, together with other potential limiting factors, determines the primary productivity of the area. Primary productivity, in turn determines the maximum sustainable density of herbivore populations. If this density exceeds the density which predatory birds and mammals require in order to survive and reproduce, natural herbivory pressure will be comparatively light. In the converse case, intense natural herbivory will be a central plant ecological factor, excluding tall woody plants (Oksanen et al., 1981).

From this, one should not conclude that forests could grow anywhere if only herbivory pressure were light. Trees face many challenges, such as surviving fires and getting the leader shoots lignified in a chilly climate. Moreover, there is no point for plants to produce tall, erect stems unless the vegetation is dense enough to generate substantial competition for light. The European experience indicates that in the long run, low herbivory pressure is a necessary condition for closed forests to persist – but not a sufficient one.

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