

Combining paleo-data and modern enclosure experiments to assess the impact of megafauna extinctions on woody vegetation

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Until recently in Earth history, very large herbivores (mammoths, ground sloths, diprotodons, and many others) occurred in most of the World's terrestrial ecosystems, but the majority have gone extinct as part of the late-Quaternary extinctions. How has this large-scale removal of large herbivores affected landscape structure and ecosystem functioning? In this review, we combine paleo-data with information from modern enclosure experiments to assess the impact of large herbivores (and their disappearance) on woody species, landscape structure, and ecosystem functions. In modern landscapes characterized by intense herbivory, woody plants can persist by defending themselves or by association with defended species, can persist by growing in places that are physically inaccessible to herbivores, or can persist where high predator activity limits foraging by herbivores. At the landscape scale, different herbivore densities and assemblages may result in dynamic gradients in woody cover. The late-Quaternary extinctions were natural experiments in large-herbivore removal; the paleoecological record shows evidence of widespread changes in community composition and ecosystem structure and function, consistent with modern enclosure experiments. We propose a conceptual framework that describes the impact of large herbivores on woody plant abundance mediated by herbivore diversity and density, predicting that herbivore suppression of woody plants is strongest where herbivore diversity is high. We conclude that the decline of large herbivores induces major alterations in landscape structure and ecosystem functions.

browsers | ecosystem functions | herbivore diversity | landscape structure | megaherbivore

During the late Quaternary, megafaunas were drastically reduced in most regions (1, 2), representing the start of an ongoing trophic downgrading that has resulted in the loss of entire functional guilds and relaxation of top-down control in today's ecosystems (3). A high proportion of the large herbivores that have survived into the Anthropocene (4) are now drastically reduced in range and abundance, rendering them functionally extinct, or have been replaced by livestock in much of their historic ranges (5–8). How has this loss of wild-living large herbivores affected landscape structure and ecosystem functioning?

Contemporary large herbivores have strong effects on the abundance of woody species, plant diversity,

nutrient cycling, and other biota (9). Most likely, the ecological effects of preextinction herbivores were as large, possibly much more so given the great size and diversity of the lost large herbivore assemblages (10, 11). We hypothesize that Pleistocene herbivore assemblages, including large and megaherbivore browsers, would have greatly reduced woody plant abundance and altered species composition and landscape structure, if present at sufficient densities. We review the impact of large herbivores (≥ 45 kg in body weight) on woody vegetation, with a focus on megaherbivores ($\geq 1,000$ kg), and combine information from modern enclosure experiments with paleoecological

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records to estimate herbivore impacts and the consequences of their late-Quaternary declines.

Impact of Large-Herbivore Assemblages on Woody Plant Abundance

Much of our understanding of the impact of large herbivores on woody vegetation comes from Africa, where the Pleistocene herbivore assemblage has remained fairly intact, albeit at a much reduced distribution and abundance (8). Exclosure studies in African savannas reveal that species-rich herbivore assemblages may reduce woody species cover by 15–95% (Fig. 1A) (12–17). This broad

range reflects factors such as body size and feeding mode (18) and soil fertility, topography, and hydrology (12, 19, 20).

African elephants (*Loxodonta africana*) have strong effects on woody plants due to their physical strength and height (21), causing disproportionate mortality of adult shrubs, by pulling them out (16), and trees, by pushing them over (22). Experiments with size-selective exclosures on savannas showed that elephants accounted for more than 80% of all woody plant loss across all plant height classes (22) whereas exclusion of elephants resulted in 42% more trees (23). Furthermore, elephants and all large herbivores debark trees and also feed on saplings and adult

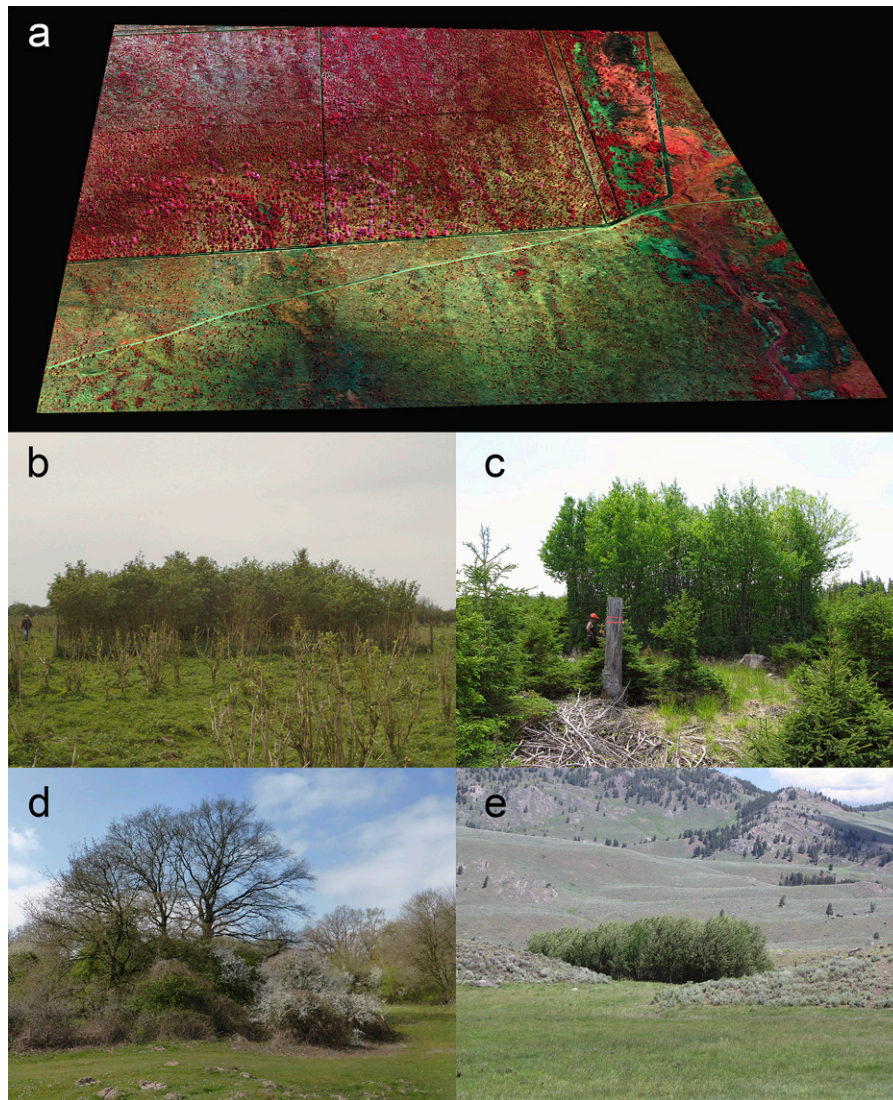


Fig. 1. Modern exclosure experiments demonstrate strong impacts of large herbivore assemblages on woody plants. (A) In subtropical savanna, a diverse large herbivore assemblage (>5 kg) greatly reduces the abundance of woody plants outside the 302-ha exclosure (upper part of the picture) (12). The 3D infrared color indicates woody vegetation (in red, more intense red revealing more gross primary productivity) and herbaceous vegetation (in green–blue). Fire is controlled both inside and outside of the exclosure [Carnegie Airborne Observatory image (122), Kruger National Park, South Africa (12)]. (B) In temperate wetland grasslands, Heck cattle, Konik horses, and red deer (*Cervus elaphus*) break down the established elderberry woodland (*Sambucus nigra*) where it is not protected by fencing (123) (Oostvaardersplassen, The Netherlands). (C) In the boreal forest, after logging, white-tailed deer strongly influence the recruitment of woody species, with the exclosure dominated by palatable deciduous species whereas a spruce parkland developed under intense browsing (38) (Anticosti Island, Quebec, Canada). (D) Thorny shrubs (*Prunus spinosa*) function as natural exclosures, where they protect establishing palatable oak (*Quercus* sp.) from herbivory (35, 47) (Borkener Paradies, Germany). (E) In temperate sagebrush and grassland vegetation, American bison (*Bison bison*) and elk (*Cervus elaphus*) strongly suppress establishment of palatable trees (*Populus* sp.), which abundantly regenerate inside the exclosure (center of the picture) (Yellowstone National Park, United States). C courtesy of Bert Hidding.

shrubs and trees without killing them, but with the effect of limiting woody plant growth and abundance (Fig. 1B) (17, 24). The removal of large browsers is thought to generally lead to a net increase in abundance of woody plants (20), but this effect depends in part on the compensatory response of smaller herbivores, which can have strong impacts, particularly on the recruitment of woody species (14, 16, 25–28).

Ground-dwelling browsers control woody plants mainly by increasing mortality in early life stages or suppressing growth to maturity by injuring plants or removing photosynthetic tissue. These impacts depend on plant height and the reach of the herbivore assemblage (29): Plants can be subject to a “browser trap” where they experience high impact while within the reach of browsers, but escape this trap by growing beyond the browse height. In species-rich herbivore communities, containing large as well as small browsers and a variety of feeding strategies, browsing impacts extend to a wider range of plant growth stages. Demographic bottlenecks imposed by browsing are therefore more difficult to escape (13, 14, 16). Temporary reductions in herbivore numbers allow trees to regenerate and grow into taller height classes, escaping herbivory by the time herbivore populations have recovered (17). Fruit and seed consumption might offset the demographic effects of browsing injury by seed dispersal, but the net effect of large herbivore assemblages on seed predation versus dispersal remains unclear (16).

The feeding mode of herbivores dictates their impact on woody plants. Browsers generally have direct inhibitory effects on growth and survival of woody plants. Grazers can suppress woody plants through trampling or occasional feeding, but can also promote recruitment and survival by reducing competition with herbaceous vegetation, thereby reducing rodent densities and reducing fire frequency by preventing fuel accumulation (15, 30, 31). Nevertheless, feeding mode impacts are complex and poorly understood because large herbivores are often mixed feeders (32).

Impact of Large Herbivores on Woody Plant Species Composition

By selecting palatable species, large herbivores affect woody species composition and promote the abundance of defended browsing-tolerant shrubs and trees (33, 34); furthermore, by creating a certain degree of vegetation openness, they promote the abundance of light-demanding woody species (35). Exclosure studies have documented these effects across a broad range of biomes. For example, in the North American boreal forest, moose (*Alces americanus*) and white-tailed deer (*Odocoileus virginianus*) selectively feed on hardwoods and the soft-needled balsam fir (*Abies balsamea*), but avoid the hard-needled white spruce (*Picea glauca*) (36), creating a spruce parkland, whereas hardwood species dominate in exclosures (Fig. 1C) (37, 38). In deciduous forest, deer browsing likewise reduces regeneration of palatable hardwood species, resulting in a more open habitat resembling oak savanna, with many light-demanding plant species (39). Browsers shift the species composition of African savanna from dominance by palatable shrubs to dominance by thorny acacias (14) and chemically defended or browsing-tolerant species (40).

Similar dynamics are seen in response to forest management. In European forest reserves, removal of domestic cattle and horses and culling of wild ungulates, such as deer and European bison (*Bison bonasus*), have resulted in the expansion of shade-tolerant tree species such as lime (*Tilia* spp.), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*), creating closed canopy

forest and out-competing the shade-intolerant oak (*Quercus* spp.) (41–44).

Spatially Structured Landscapes

In landscapes characterized by intense herbivory, woody plants can persist by defending themselves, by associating with defended species, or by growing in areas that are physically inaccessible or that are risky for herbivores because of high activity of predators (34, 45). The resulting variation in the local intensity of herbivory can create spatial mosaics of herbaceous plants, shrubs, and trees.

Palatable woody species can regenerate in the vicinity of thorny or poisonous forbs and shrubs that protect them from browsing (Fig. 1D) (46–48). Cyclic succession may occur as grasslands are colonized by thorny shrubs, from which palatable trees can grow, which outcompete the shrubs; with death of the trees, herbivory suppresses woody plant regeneration, returning the system to a grassland state. Because, spatially, patches are out-of-phase over time, this cyclic succession may result in a mosaic of grasslands, shrubs, single trees, and clumps of trees at the landscape scale (35).

Alternatively, palatable species may grow in areas that are physically inaccessible, such as steep slopes or between rocks and logs (49, 50). Spatial heterogeneity in landscape structure can also be induced by the presence of predators imposing a landscape of fear (51). As a response to perceived predation risk, often heterogeneously distributed across the landscape (52), herbivores may select less risky areas, creating spatial variability in herbivore pressure and thus varying impacts on vegetation (34, 53). Therefore, the presence of predators can allow local increases in the abundance of woody species, such as observed after the introduction of wolves in temperate woodlands followed by reduced browsing pressure from deer and locally enhanced recruitment of palatable shrubs and trees (45, 54–56), resembling that observed in exclosures (Fig. 1E).

Because extremely large size confers a high degree of invulnerability to predation (21), adult megaherbivores may prefer areas with a higher density of trees, because of greater forage availability, whereas smaller herbivores often prefer open grassland due to higher risk of ambush by predators in the woodland (53). As a result, assemblages of different-sized herbivores will exert spatially heterogeneous grazing and browsing pressure across the landscape, which affects woody plant abundance and species composition (34).

How Did Extinct Late Pleistocene Megaherbivores Affect Woody Plants?

The interpretation of extinct megaherbivore impact relies on the comparison with the ecology of modern megaherbivores. There are 8 extant megaherbivores, from three orders (Cetartiodactyla, Perissodactyla, Proboscidea), and 35 extinct megaherbivores from the Late Pleistocene, from seven orders (Cetartiodactyla, Cingulata, Diprotodontia, Notoungulata, Perissodactyla, Pilosa, and Proboscidea) (1). An open question is whether extinct megaherbivores would have had similar effects on woody plants as their contemporary closest relatives. The nine extinct Late Pleistocene proboscideans had divergent feeding strategies, from the predominantly grazing woolly mammoth (*Mammuthus primigenius*) to the browsing American mastodon (*Mammuthus americanum*) (57–59), the latter being supposedly most similar in feeding ecology to present-day browsing black rhinoceros (*Diceros bicornis*) or moose (*A. americanus*) (60, 61). Whereas

some niche separation was evident (57, 61, 62), recent multiproxy data on megaherbivore paleodiets suggests that many were mixed feeders that adapted their diets to local plant availability (62–64). Similarly, extant megaherbivores are mostly mixed feeders with a few grazing specialists like the hippopotamus (*Hippopotamus amphibius*) and white rhinoceros (*Ceratotherium simum*) (65). Further work comparing the guild structures of megaherbivores both in the present and the Late Pleistocene would provide better understanding of the potential impact of these species on vegetation structure.

Extinct megaherbivores would have impacted woody plants through consumption, but also by other physical impacts. Wear patterns on the teeth and tusks of mastodons have been interpreted as indication of their bark stripping behavior (60, 66), which would undoubtedly have killed many trees and shrubs as observed with contemporary African elephants (59). Selective feeding of mastodons on spruce may have contributed to the spruce–pine transition in the US Great Lakes region in the Late Pleistocene (57). Furthermore, many extinct and extant megaherbivores are avid fruit consumers and thus contributed strongly to the abundance of woody plants through dispersal of fruits, in particular those that bear the megafaunal dispersal syndrome (67, 68).

The paleoecological record provides evidence of geomorphological engineering by mammoths, presumably digging for water and mineral-rich sediments, trail formation, and trampling, similar to what elephants do today (69). Combined geo-engineering and enhanced nutrient cycling by extinct megaherbivores would have significantly contributed to the maintenance of open habitats, dominated by fast growing palatable herbaceous vegetation over slower growing woody species (59, 70). The impact of Pleistocene herbivore assemblages may have

been amplified by lower atmospheric CO₂ concentrations during glacial episodes. Low CO₂ probably limited woody plant growth, impeding recovery from herbivory and increasing total impact of herbivores (71, 72).

Evidence of Large-Herbivore Impact from the Paleoecological Record

The extinction and density reductions of Late Pleistocene large herbivores represent a grand removal experiment (1). We assess this experiment by comparing landscape structure and vegetation composition in the presence and absence of Late Pleistocene diverse large-herbivore faunas over time, under more or less similar climatic conditions. Similarities between patterns of woody plant response to large herbivore removal in the paleoecological record and modern exclosure experiments are indicated in Table 1.

The initial ecological adjustment of plant communities to release of browsing and grazing after megafauna extinctions should be completed within relatively short periods of decades or centuries and can thus seem rapid in paleoecological records spanning thousands of years. After that, long-term changes, such as through reduced seed dispersal, would continue to influence plant species distributions up until present times (67). The ecological consequences of megafaunal extinctions have received little study, which is in part due to limitations inherent to comparing a discontinuous vertebrate bone record with a vegetation record constructed primarily from lake sediment records that are typically not associated with megafaunal fossils. Recently, the use of *Sporormiella* and other coprophilous fungi has shown promise for determining the abundance of large herbivores and testing their impact on vegetation in the paleoecological record. *Sporormiella* spores are preserved in lakes and mires along with pollen

Table 1. Examples of the impact of large herbivores on woody plants, species composition, and landscape structure as found in contemporary (exclosure) studies and from the paleoecological record

Process	Contemporary pattern	Paleoecological record
Large herbivores reduce the abundance of woody plants.	Higher woody plant cover in exclosures and after removal of large herbivores (12–16)	Landscapes of previous interglacials seem to have been more open than after Pleistocene extinctions in the early Holocene (81, 82). Moas may have maintained mosaics of open canopied woodland and scrub (95).
Large herbivores induce shifts in woody species composition.	Under intense browsing, unpalatable and thorny species thrive and palatable species are suppressed (14, 37, 40). Browsing may also promote browsing-tolerant species (102). Under intense herbivory, light-demanding trees and shrubs are promoted (35, 39).	Increase in palatable and shade-tolerant hardwoods immediately after the Pleistocene extinction in North America (75, 78). Increase in unpalatable trees during historically high herbivore densities in European forest (111).
Large herbivore impact is mediated by soil fertility.	More thorny shrub species in fertile habitats may indicate higher browsing pressure (35). Higher elephant impact on treefall at fertile soils (22)	Vegetation openness was greater in fertile lowland areas, compared with less fertile upland areas (82).
Herbivores modify vegetation responses of woody plants to climate and soils.	In tundras, herbivores can inhibit shrub encroachment with climate warming (87), but this effect is site-dependent (88). In savannas, woody species cover does frequently not reach its abiotic potential due to fire and herbivory (115, 116).	Mosaic forest tundra in northeastern Siberia during the Last Interglacial, with browsing tolerant trees frequent—likely (at least partly) due to large herbivores (86). Large herbivore presence maintained the mammoth steppe in northeastern Siberia, which disappeared after Late Pleistocene extinctions (70, 85). Higher openness of vegetation in last interglacial than expected based on climate and soil may be mediated by large herbivores (81).
Herbivores reduce fuel load for fires.	Herbivores reduce herbaceous biomass and fire frequency, which benefits woody species, unless these woody plants are also browsed (30, 116, 117).	Increased fire activity immediately after the Pleistocene extinctions (73–76, 78)

and so can be used to provide the ecological context of functional large herbivore collapse (73–77).

Several pollen records from eastern North America show an increase in hardwood deciduous taxa immediately after the *Sporormiella*-indicated megafaunal decline, including increases in palatable and shade-tolerant woody species (74, 75, 78), and a more closed vegetation, consistent with release from browsing pressure. The continued postextinction presence of light-demanding oak (*Quercus alba*) indicates that the surviving large herbivores could have maintained a certain degree of openness of the landscape (42), which has also been ascribed to the effect of dry climate and anthropogenic fires (79). Similarly, the now-endangered grass balds of the southern Appalachian mountains are hypothesized to be remnants of past herbivory (later maintained by Native American burning) (80).

Pollen and *Sporormiella* records from northeastern Australia (76) during the last glaciation record a decline of large herbivores around 40,000 years ago, followed by a shift from a mixed and relatively open vegetation, consisting of elements of angiosperm and gymnosperm rainforest along with sclerophyll species, to pure sclerophyllous vegetation, in apparent absence of major climate change. This vegetation shift was evidently due to a combination of relaxed herbivory pressure and increased fire that closely followed the onset of herbivore decline (76).

Evidence from fossil beetles indicates that regions of European vegetation were more open in the Last Interglacial and supported more dung beetles, than after the extinctions, in the pre-agricultural Holocene. Some wood-pasture and moderate open vegetation remained in the early Holocene, indicating a role for the remaining wild herbivores (81–84).

In northeastern Siberia, the productive pastures of the mammoth steppe disappeared after the removal of the high densities of large herbivores that may have maintained this ecosystem and was replaced by mossy forests and tundras (85, 86). The modern climate of this area is inside the mammoth steppe climatic envelope, suggesting that the removal of high densities of large herbivores determined the biome transition from pasture to tundra with woody plants (70). Modern experiments show that herbivores can inhibit shrub encroachment on tundra with climate warming, but this effect is site-dependent (87, 88).

The presence and loss of megafauna might also have long-term impacts on biotic communities that are still ongoing and witnessed by current plant traits that coevolved with megafauna, which may be less adaptive in modern landscapes (e.g., ecological anachronisms) (89). For example, woody species that are adapted to megafauna dispersal (67) may still be experiencing slow declines (90), depending on whether megafauna have been substituted by smaller wild animals, domestic livestock, or humans. Similarly, coevolution with the recently exterminated moa and elephant birds, flightless ratite birds 20–500 kg (91), can explain some remarkable idiosyncrasies of New Zealand and Madagascar vegetation, especially the high representation of “wire plants,” a growth form likely to have reduced the foraging efficiency of moa, thus providing protection from browsing (92–94). Browsing by moa might also have created canopy gaps that sustained high diversity of light-loving herbs and regeneration of light-demanded conifer seedlings (95).

In summary, modern studies and paleo-studies indicate that removal of large herbivores is followed by increased abundance of woody plants and altered vegetation composition and structure toward less open landscapes, with more shade-tolerant and palatable species (Table 1).

Under What Conditions Would Pleistocene Large Herbivore Assemblages Have Had Most Impact?

Based on the evidence from modern enclosure studies and the paleoecological record, we expect that the Late Pleistocene large herbivore assemblages would have had at least equal, but probably stronger impacts on woody plant abundance than most contemporary assemblages, due to their broader range of body sizes and higher species-richness imposing more complete inhibition of woody plant life stages (Fig. 2). However, a central question that needs to be answered is under what conditions were herbivore densities high enough to have strong impacts on landscape structure.

Landscape geomorphology plays an important role in sustaining particularly megaherbivore densities because these animals often tend to avoid steep slopes. Therefore, high concentrations of large herbivores are more often found in a plains habitat than in steep terrain, both in modern times and in the Pleistocene, resulting in higher impacts on woody plants and greater openness on plains (96, 97). The effect of terrain may be amplified by hydrology because both modern and Pleistocene large and megaherbivores frequently visit water bodies, resulting in enhanced local landscape openness around fresh water (98). Modern large herbivore communities reach their highest densities and diversities at sites of high soil fertility, due to high food quantity and quality (99, 100). Plant traits confirm this pattern because woody species in fertile areas defend themselves heavily with thorns or tolerate herbivory through rapid growth, indicating adaptations to high browsing pressure (35, 47, 101, 102). Similarly, during the Last Interglacial, open vegetation was found in European lowlands whereas less fertile uplands were more wooded, suggesting a larger herbivore impact in fertile habitats (Table 1) (82).

Although the places in the landscape attracting the highest densities of large herbivores can be identified, the absolute densities and the fluctuations therein of Pleistocene large herbivore assemblages remain difficult to determine. In the Late Pleistocene, communities of large predators were also more diverse than today, and they probably limited the densities or habitat use of large herbivores (103). Despite this predator diversity, Late Pleistocene densities of large herbivores at the mammoth steppe in Alaska and northeastern Siberia have been estimated at 88 and 105 kg·ha⁻¹, respectively, during the Last Glacial (61, 85). In the Last Interglacial in Great Britain, densities were estimated at ≥ 2.5 large ungulates per hectare in over half of the studied sites (81), which amounts to ≥ 125 kg·ha⁻¹ (at a mean ungulate weight of 50 kg). These densities of Pleistocene large herbivores are in the range of the African game reserves (9–191 kg·ha⁻¹ [in Pachzelt et al. (104)] and imply strong impacts on woody plants. They also suggest that at least some landscapes were kept open by herbivory, given that to allow regeneration of modern temperate closed-canopy forests herbivore densities (deer) have to be very low (<3.5 kg·ha⁻¹) and that at densities of >25 kg·ha⁻¹ the forest is transformed toward oak savanna or wood-pasture (39). The temperate wood-pastures, in turn, respond fundamentally differently to herbivory than closed-canopy forests because here trees can persist by regeneration within light-demanding thorny shrubs, also in the presence of high densities of large ungulates at fertile soils (110–187 kg·ha⁻¹) (35, 47, 105, 106). More estimates of densities of Pleistocene herbivores would greatly advance our understanding of their ecological impacts.

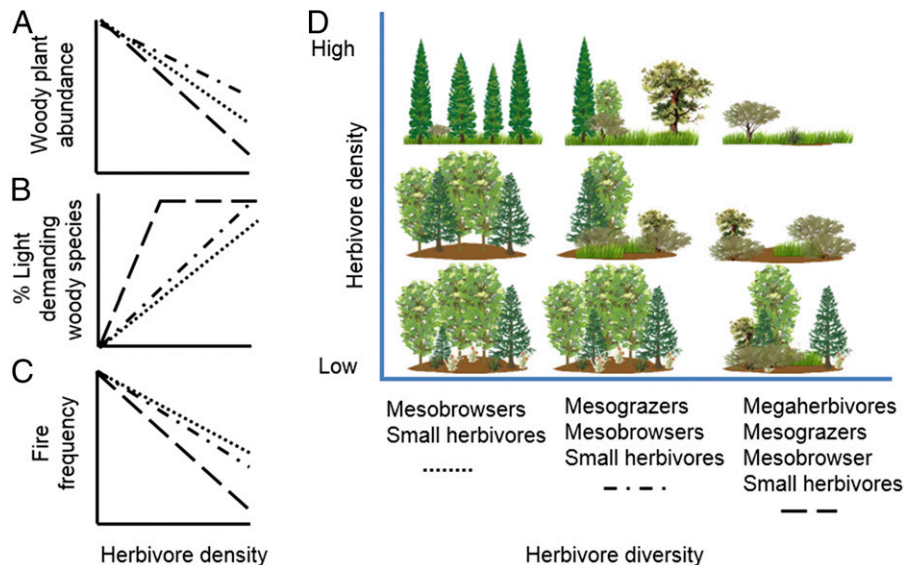


Fig. 2. Hypothesized impact of large herbivore removal on landscape structure, proportion of light-demanding woody species, and fire frequency. All of these landscapes represent sites where the climate and soil allow trees to dominate. The dotted and dashed lines in A–C correspond to the three herbivore assemblages indicated on the x axis of D. The three herbivore combinations represent a series of herbivore diversity indicating simplification from the full Pleistocene fauna to the common late Holocene condition. We predict that removal of megaherbivores would result in (A) increased woody plant abundance, (B) reduced percentage of light-demanding species, and (C) increased fire frequency, depending on the densities of the remaining wild herbivores. (D) The resulting landscape structure. In essence, over time, the landscape developed in many areas from open in the Late Pleistocene, with high densities of diverse herbivore assemblages (D, Top Right), to defaunated wild herbivore communities controlled at low densities in the Holocene, resulting in a wooded landscape (D, Bottom Left), unless livestock is introduced, which could take over the role of native extinct grazers, resulting in a wood pasture (D, Middle). In the wood pasture, palatable light-demanding trees can regenerate within the protection of light-demanding thorny shrubs. When browsers are not managed, they can reach high densities, resulting in an open landscape with unpalatable, light-demanding trees (D, Top Left).

Perspectives for Future Research

The paleoecological record provides several examples that support the hypothesis that the Quaternary extinctions of megaherbivores rapidly changed vegetation composition and structure in different regions, but further tests are needed to confirm the generality of these findings. We propose the following approaches to provide such evidence.

Geographically Spread Paleoecological Records. More detailed, chronological records of herbivore abundance and vegetation change from the Late Pleistocene-to-Holocene transition are needed to determine whether herbivore decline preceded vegetation change or not. Sampling more lake and peatland cores for both pollen and *Sporormiella* would yield such data to allow generalization of the few currently available studies (75, 76), taking into account improvements in the calibration of *Sporormiella* (77). Furthermore, comparisons of landscape openness and herbivore abundance before and after megafaunal extinctions under similar climatic conditions yields evidence of the impact of large herbivores [e.g., Sandom et al. (81)]. In both cases, the use of multiple proxies for herbivore density and abundance of woody plants would be valuable (Table 2) because each proxy will have its own limitations. Proxies need to be calibrated with modern data. Geographical spread of the sample locations across continents would allow for further generalization of herbivore impact across taxonomically very different faunas. These samples should be distributed over gradients of climate, fertility, and topography to assess the abiotic factors governing the impact of large herbivores on vegetation.

Large-Scale Modeling. Modeling climate envelopes in which biomes occur, when regulated by climate conditions alone, allows

identification under what conditions large herbivore impacts would potentially make a strong difference. Especially where alternative vegetation states are climatically possible, this approach generates testable hypotheses about the impact of herbivores, such as in the case of the mammoth steppe and savannas (85, 107). These hypotheses could subsequently be addressed either by adding herbivores in the model, using literature data or performing experiments. Similarly, the present-day landscape structure and woody species composition can be linked to abundance and species richness of large herbivore assemblages over large biogeographical areas [see, for instance, Greve et al. (108)]. This relationship will yield baseline data that can be applied to Late Pleistocene conditions to predict what the landscape structure was, given estimates of large herbivore abundances. Furthermore, mechanistic models can be used to predict the interaction between herbivore communities and vegetation. Recently, large-scale coupling of physiologically based vegetation and herbivore population models has been applied to predict herbivore population dynamics at continental scales (104). This approach could also be used to predict herbivore impact on the vegetation.

Experiments. Because woody species have long generation times and spatial heterogeneity in landscape structure is a key feature of wooded habitats under herbivory, small-scale and short-term exclosures may capture only part of the resulting woody plant dynamics at the landscape scale. Therefore, long-term and large-scale experiments—including unintentional experiments—are extremely valuable to determine large herbivore impact on woody plants (12). These conditions can be found, for instance, at the Finnish–Russian border [which had markedly different reindeer densities across the border (109)], in ongoing and

Table 2. Characteristics of a herbivore-influenced landscape that can be found in the paleoecological record

Component	Large herbivore-influenced landscape has	Proxies in the paleoecological record
Herbivores	Presence of large herbivores	Fungi: dung fungi spores (77, 118) Fossil beetles: dung beetles (81, 119) Herbivores: fossil remains of herbivores or dung (61, 66, 85) Fossilized herbivore tracks (69, 98)
Vegetation composition	Light-demanding plant species Thorny, unpalatable or herbivory-tolerant plant species Higher ratio of C ₄ grasses over C ₃ forbs	Plants: pollen, macrofossils, ancient DNA, stable isotopes (63, 75, 76, 120)
Woody plant abundance and landscape structure	Landscape openness where climatic conditions predict more closed woody plant cover	Fossil beetles: proportion of wood beetles from terrestrial beetles (83, 84) Plants: pollen, macrofossils, ancient DNA, stable isotopes to determine woody plant abundance (delta ¹³ C) (121) Other fauna: bat species associated with open or more wooded landscapes (120)
Plant biomass	Reduced plant biomass and low fire frequency in fire-prone landscapes	Charcoal (10, 75)

Single characteristics may also be caused by other factors: in particular, fire and climatic conditions. The combination of properties should provide clues to the likelihood of large herbivores or other factors driving the observed patterns, which could further be tested by large-scale modeling or experiments, combining modern ecology and paleoecology.

future rewilding projects (110), and in forest reserves where large herbivores were removed to protect tree regeneration (42). In this respect, the forestry literature may offer valuable information about the regeneration ecology, competitive ability, and herbivore tolerance of woody species (42, 44). Such long-term fencing studies are also very useful to test proxies for herbivore and woody species abundance in an experimental setting (111).

Study of Contemporary Large Herbivore-to-Megaherbivore Impacts. Studies on current megaherbivore impacts are extremely valuable because these animals are the only proxies that we have for extinct megafauna. Better insight into the behavior, habitat preferences, and whole ecosystem functions of large herbivores is required (112) to predict their impact on landscape structure. Because most are experiencing alarming declines, some may already be too rare to study whereas, for several species, the wider impacts of their ecosystem engineering effects only very recently have started to become clear (8, 113, 114).

Conclusions

Given the ecological importance of modern large herbivores, we see the end-Pleistocene reduction in diversity and biomass of such animals as being a significant event in global ecology. Growing evidence supports the hypothesis that the loss of large herbivores strongly affected woody plants and triggered regime shifts across the World's biomes. Linking large herbivores and their impact on vegetation at Quaternary timescales is an enormous task, but an

interdisciplinary approach that combines proxy records and modeling grounded by modern studies will help to link pattern and process in the paleoecological record (Table 2). Modern large herbivores are now among some of the most threatened species, facing the combined threats of anthropogenic land use and climate change (8). The ecological consequences of the end-Pleistocene extinctions are therefore relevant not only to understanding the vegetation changes of the early Holocene, but also to the management of ecosystems in the Anthropocene. In this respect, modern and paleoecological analyses have much to contribute to one another. Testing hypotheses to explain the variation in effects of large herbivores and their decline on woody plants and landscape structure should be a priority for future work. This hypothesis testing should integrate the effects of fire and herbivory across large abiotic and geographical gradients to obtain a better understanding of herbivore regulation of woody plants and the importance of herbivore body size, density, and diversity.

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