Review

Mitigating Human Effects on European Biodiversity through Traditional Animal Husbandry

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Abstract: *Livestock grazing (without modern fertilizers), mowing, and other traditional methods of animal husbandry are used in Europe for managing human-made habitats such as seminatural grasslands. From a review of essential literature, I hypothesize that traditional animal husbandry partially compensates for the loss of natural processes that have been suppressed by humans. There is indirect evidence that livestock grazing and mowing have made possible the continued existence of many species threatened by the human overkill of megaherbivores and other large herbivores. Many species that were dependent on natural fires and floods may have benefited from grazing and mowing, which also may be effective tools for mitigating the negative effects of eutrophication. As partial surrogates, traditional grazing and mowing have obscured the importance of natural disturbances to European biodiversity. Thus, the end of traditional animal husbandry, together with the suppression of natural disturbances, may cause even more adverse effects to biodiversity than is generally recognized.*

Mitigación de los Efectos Humanos sobre la Biodiversidad Europea Mediante la Producción Tradicional de Animales

Resumen: *El pastoreo de ganado (sin fertilizantes modernos), el segado y otros métodos tradicionales de producción animal son usados en Europa para el manejo de hábitats creados por humanos tales como los pastizales seminaturales. A partir de una revisión de la literatura esencial, planteo la hipótesis que la producción tradicional de animales compensa parcialmente por la pérdida de procesos naturales que han sido suprimidos por humanos. Existe evidencia indirecta de que el pastoreo y el segado ha hecho posible la existencia continuada de muchas especies amenazadas por la eliminación excesiva de megaherbívoros y otros herbívoros grandes. Muchas especies que dependían de incendios naturales e inundaciones, se han beneficiado del pastoreo y el segado, lo cual puede ser también una herramienta efectiva para mitigar los efectos negativos de la eutroficación. Como sustitutos parciales, el pastoreo tradicional y el segado han confundido la importancia de las perturbaciones naturales sobre la biodiversidad europea. Por lo tanto, el fin de la producción animal tradicional junto con la supresión de perturbaciones naturales puede causar efectos sobre la biodiversidad aún más adversos de lo que generalmente se reconocen.*

Introduction

In the European agricultural landscape, seminatural grasslands—permanent unfertilized pastures and meadows formed by traditional agricultural methods—are valuable habitats for nature conservation (Duffey et al. 1974; Bakker 1989). Their decline has been severe during recent decades, however, because of the intensification of agricultural methods and the abandonment of traditionally used areas (Hillier et al. 1990).

Traditional livestock grazing and mowing are widely used to maintain high biodiversity or rare species. Their similarities to natural processes are rarely recognized, however, so the importance of traditional animal husbandry as a conservation tool is underrated. I hypothesized that in Northern and Central Europe methods ap-

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plied in traditional animal husbandry partially replace several human-suppressed and important natural processes that maintain biodiversity and mitigate other deleterious human effects. Because of the similarities between the effects of natural disturbances and animal husbandry, traditionally managed habitats can harbor many features of pristine habitats.

Because modern agriculture usually employs intensive methods and inorganic fertilizaters harmful to biodiversity, a clear distinction between it and traditional animal husbandry must be made. I define traditional animal husbandry as livestock grazing, mowing, and other methods (excluding plowing and seeding) of supplying food, fences, and shelter for animals in a way developed before the industrial revolution, methods that cause no nutrient enrichment to managed seminatural areas. My hypothesis has a speculative flavor because empirical data on the ecological effects of most natural disturbances to European ecosystems are largely lacking. However, if further studies justify this hypothesis, it would encourage new succesful biodiversity management in Europe and elsewhere.

History of Land Use and Vegetation

Until the nineteenth century, most of the land in Europe was used for traditional animal husbandry (Ellenberg 1988; Emanuelsson 1988). Because of differences in climate and the size of human populations, land management in different parts of Europe varied in many respects. A crudely simplified picture of land-use practices can be given for Northern and Central Europe. Most herbaceous vegetation (mires, shores, etc.) were used as hay meadows and/or pastures, and many forests and other partially forested areas were cleared to form meadows, often with the help of fire (Ellenberg 1988). Winter fodder for animals was collected from meadows and from pollarded and coppiced trees. Cattle grazed almost everywhere in the forests (Rackham 1995). Other commonly used methods for vegetation manipulation were cutting of trees and bushes, burning, and irrigation of hay meadows (Ellenberg 1988; Rackham 1995). Many areas were occasionally plowed, and fields were grazed when fallow. Fertilization of arable crops with animal manure caused a nutrient shift from grazed grasslands and forests to cultivated fields (Emanuelsson 1988). As a result, nutrient depletion occurred over time in most of the seminatural areas (Emanuelsson 1988).

Most ecologists in Europe agree that traditional livestock grazing and hay removal maintain and/or increase the richness of plant species and are important for the maintenance of animal species diversity (Duffey et al. 1974; Hillier et al. 1990). Plant succession results in the loss of many species after abandonment of the traditional methods; thus, seminatural habitats, although human-made, have high priority in nature conservation (Duffey et al. 1974; Bakker 1989).

Most species of permanent grasslands and other seminatural grazed and mowed habitats are indigenous to an area; Central Europe is a good example (Ellenberg 1988). Why do so many indigenous species benefit or depend on traditional animal husbandry?

It is generally thought that during the Holocene, before human-made clearances, forests covered most of Europe and primary grassland vegetation was rare (Rackham 1995). Natural grasslands occurred mainly on floodplains and other wetlands, mountains, cliffs, and other skeletal or toxic soils (Ellenberg 1988). Recently, the hypothesis of closed-forest domination has come into question mainly because most species do not grow in closed forests but in semi-open or open areas (Andersson & Appelqvist 1990; Rose 1992; Wallis de Vries 1995). Few vascular plants in Central Europe prefer shade (Ellenberg 1990; Ellenberg et al. 1991). The abundance of species in semi-open forests does not prove that closed forests were not dominant, but it serves as evidence of the crucial importance of natural disturbances to European ecosystems. A large proportion of woodland species thrive in open, sunny conditions, suggesting that primeval forests may partially have more resembled pasture-woodlands than closed-canopy forests (Rose 1992).

Fires, storms, floods, landslides, and beavers (*Castor fiber* in Europe and *Castor canadensis* in North America) created a variety of gaps in forested landscapes (Ellenberg 1988). Short-term grassland vegetation in the forest gaps may have been fairly common, forming the original habitats of many plants and animals regarded as grassland species (Nilsson & Ericson 1997). It has been argued that most of these primary grasslands in Europe have been destroyed by humans and that the existence of many grassland species depends upon seminatural grasslands (Erhardt & Thomas 1991; Klemm 1996). Several authors have also pointed out that grazing cattle compensated for the loss of many native large herbivores (Ridley 1930; van Wieren 1995; Wallis de Vries 1995; Olff et al. 1999).

Large Herbivores

It seems probable that humans played an important role in the mass extinction of mammals at the end of the Pleistocene in Eurasia, North and South America, and Australia (Martin & Klein 1984). Owen-Smith (1987) has shown that megaherbivores (mammals exceeding 1000 kg in body mass) were keystone species that could turn a closed forest into an open, park-like woodland or grassy savannah, at least in arid regions. There is no convincing evidence that large herbivores created grasslands or savannah-like woodlands in Europe, although several authors have suggested it (Andersson & Appelqvist 1990; Wallis de Vries 1995; Olff et al. 1999). There is support, however, for the hypothesis that the European landscape changed after the depauperation of the mammalian fauna. Grassland plants were more abundant during the earlier interglacial periods than from 10,000 to 4,000 B.C. (Rackham 1995). Native large herbivores left in Europe are important in determining the structure and species composition of forests and in prolonging the life span of grassland gaps (Faliński 1986; Kirby et al. 1995; Olff et al. 1999). Large herbivores may also increase the persistence of the effects on vegetation of natural disturbances such as fire and floods (Ellenberg 1988; Nilsson & Ericson 1997).

Many European plants have adaptations that reduce the potential harmful effects of grazing and amplify the dispersal of plant propagules with large grazing animals. For example, a biennial grassland plant, *Gentianella campestris*, may even show overcompensation, or increased fruit and seed yield as a consequence of grazing damage (Lennartsson et al. 1998). This shows that the long history of coevolution with large mammalian herbivores is still visible in the European flora. Andersson and Appelqvist (1990) have even suggested that ancient agriculture with grazing livestock saved a large proportion of the grassland flora that had adapted to grazing by indigenous herbivores. The importance of livestock as seed dispersers in place of extinct herbivores has been noted by several authors (Ridley 1930; Janzen 1982). Fischer et al. (1996) exemplified the efficiency of seed dispersal by livestock: a single sheep transported over 8500 diaspores of 85 vascular plant species in its fleece during one summer.

Mammalian herbivores become less selective of plant material as body size increases (Demment & van Soest 1985). Most ruminants in the Northern hemisphere are selective feeders: concentrate selectors (browsers, such as roe deer [*Capreolus capreolus*] and moose [*Alces alces*]), intermediate feeders (red deer [*Cervus elaphus*], European bison [*Bison bonanus*] and goat [*Capra hircus*]), or selective grass-roughage eaters (sheep [*Ovis aries*]) (Hofmann 1985). The only nonselective grass-roughage eaters in Europe highly adapted to digest forage rich in fiber were aurochs (*Bos primigenius*), which are extinct, and domestic cattle (Hofmann 1985). Nonselective feeding behavior leads to the suppression of large and abundant plants. This in turn increases plant diversity (Hulme 1996). The feeding behavior of aurochs, and probably of megaherbivores in general, suggests that they were beneficial for biodiversity. Because the keystone species, aurochs and tarpan (*Equus ferus*), are extinct, ecological substitutes for them, cattle and horses, should be used in nature conservation (van Wieren 1995; Wallis de Vries 1995; Olff et al. 1999).

Fires

Fire was an key ecological process for maintaining biodiversity on a landscape scale in Europe, particularly in the boreal zone (Zackrisson 1977; Esseen et al. 1997). Fire suppression by humans has been efficient in Northern and Central Europe. For example, in recent decades only 0.001–0.02% of forest acreage has burned annually in Sweden (Esseen et al. 1997).

There are many similarities between the ecological effects of herbivores and fire (Bond & van Wilgen 1996), but also many differences (Hobbs 1996) (Table 1). Mowing often accomplishes most of the conspicuous changes caused by fire (Daubenmire 1968). Although more studies are needed, it appears that many European plants indigenous to fire-prone habitats or otherwise increased by burning, benefit from grazing and mowing.

Without livestock grazing and mowing, the cooling of climate during the Holocene would have led to the extinction of many thermophilous species in Northern Europe (Thomas 1993). Eighteen percent of the British butterfly fauna depend on traditional grassland management, which reduces the height of the vegetation and results in a warmer microclimate in the summer (Thomas 1993). *Maculinea arion* is a classic example of a management-dependent species, which in the United

Table 1. Similarities between the ecological effects of fires and of traditional livestock grazing and mowing.*

Ecological effect	*Fire*	*Grazing and mowing*
Defoliation	+	+
Biomass cover of live and standing dead plants	−	−
Litter cover	−	−
Trees and bushes	−	−
Spruce	−	+ (grazing) − (mowing)
Deciduous trees	+	−
Light availability	+	+
Warm microhabitats	+	+
Longer growing season	+	+
Gaps in the vegetation	+	+/−
Nutrient cycling	+	+
Available nutrients	+	− (+)
Aboveground production	+	− (+)
Seed-dispersal distances	+	+
Seedlings of plants	+	+
Flowering of plants	+	−
Allelopathic chemicals in soils	−	0
Compaction of soils	+	+
Erosion	+	+
Rise of soil pH	+	0/+
Physical weathering of rock surfaces	+	0
Landscape-level heterogeneity	+	+

**Compiled from Daubenmire 1968; Duffey et al. 1974; Rundel 1981; Bakker 1989; Thomas 1993; Whelan 1995; Bond & van Wilgen 1996. Symbols: +, increase; −, decrease; 0, no response.*

Kingdom is confined to effectively grazed (vegetation grazed to <3 cm tall), south-facing slopes (Thomas et al. 1998). In Finland *M. arion* is found on southern slopes of semi-open pine forests on sandy eskers, and the species is threatened because of the elimination of forest fires (Kolev 1998). This example suggests that the thermophilous fauna was originally dependent on fires and other natural disturbances. Because the natural disturbance regime ceased long ago, many thermophilous species may now depend on human-made disturbances such as livestock grazing.

Floods

Humans have tried to prevent floods by regulating the water level of lakes and rivers and the drainage of wetlands. As a result, the conditions of most European wetland ecosystems have changed (for rivers see Dynesius & Nilsson 1994). Natural floods act as geomorphic disturbances creating herbaceous wetland vegetation. Before regulation, river dynamics in the flood plains of large rivers created a variety of dynamic grassland habitats (Klemm 1996). With the prevention of spring floods, however, the extent of natural alluvial grassland along river and lake shores has decreased. The decrease in naturally formed wet grasslands has been largely offset by the use and creation of wetland meadows (Klemm 1996). Thus, livestock grazing has been beneficial to the biodiversity of North and Central European shorelines (Dijkema 1990).

Table 2. Relationship between various ecological effects and traditional grazing and mowing or eutrophication.[a]

Ecological factors	*Grazing and mowing*[b]	*Eutrophication*[c]
Small-scale structural diversity	+	−
Light, temperature radiation	+	−
Temperature oscillations	+	−
Moisture oscillations	+	−
"Continentality"	+	−
Net primary production	−	+
Amounts of available nutrients	−	+
Abundance of reed	−	+[d]
Effect of natural physical disturbances	+	−

[a] *Symbols: +, grazing and mowing or eutrophication increases the ecological factor considered; −, grazing and mowing or eutrophication decreases the ecological factor considered.*
[b] *Compiled from several sources (e.g., Bakker 1989; Dijkema 1990; Hillier et al. 1990; Stoutjesdijk & Barkman 1992; Thomas 1993).*
[c] *From Ellenberg (1990).*
[d] *From Björk (1967).*

Eutrophication

Eutrophication is one of the most severe problems for biodiversity in Europe (Ellenberg 1990; Thompson 1994). The majority of the vascular plants native to Europe are restricted to less productive habitats (Hodgson 1987; Ellenberg 1990). Nutrient enrichment (mainly nitrogen and phosphorus) increases primary production and decreases plant diversity in most environments (Tamm 1991).

Mowing and grazing have resulted in a significant removal of nutrients in some studies (Marss 1993). In this respect, mowing is more effective than grazing. In many eutrophied habitats, both measures can be used to mitigate the effects of nutrient enrichment (Table 2; Anderson 1995) because they effectively decrease the standing crop and control species assemblages (Bakker 1989; Jefferies & Maron 1997).

Eutrophication of waters is probably an important factor (together with the cessation of grazing) in the significant increase of reed (*Phragmites australis*) in Northern Europe (Björk 1967; Puurman & Ratas 1995). The expanding area covered by reeds has caused a decline in the population of many species typical of low-growing vegetation along shores. Grazing and mowing prevent the expansion of reeds. Similarly, grazing can promote the existence of the halophytic vegetation and the specialized fauna and flora of salt marshes (Dijkema 1990). Decreases in the populations of halophytic plants have occurred on the brackish shores of the Baltic, caused by eutrophication, drainage, and other human-induced changes. Vascular plant species assemblages of Finnish grazed, soft-bottom seashores can be floristically similar to those of pristine seashores. Most vascular plants of soft-bottom seashore grasslands would benefit from cattle grazing (Fig. 1).

Eutrophication also speeds up overgrowth and increases the standing crop in fens, thus reducing species richness (Wheeler et al. 1995). Most rare fen species occur in species-rich fens with a low standing crop (Wheeler 1988). Grazing and, particularly, mowing can mitigate the effects of eutrophication (Wheeler 1988; Vermeer & Joosten 1992). Therefore, they can be used as management tools to maintain the original species-rich vegetation (Wheeler 1988; Verhoeven et al. 1996).

Eutrophication causes a shift toward more maritime Atlantic conditions because the height of the vegetation increases and the climate of the habitat becomes cooler and moister (Ellenberg 1990). Ellenberg (1990) has shown that in Central Europe the plants requiring a continental microclimate (much light, high temperature) are more threatened than those requiring an Atlantic microclimate. Grazing and mowing cause a shift toward continental microclimate (Thomas 1993), mitigating the microclimatic changes caused by eutrophication.

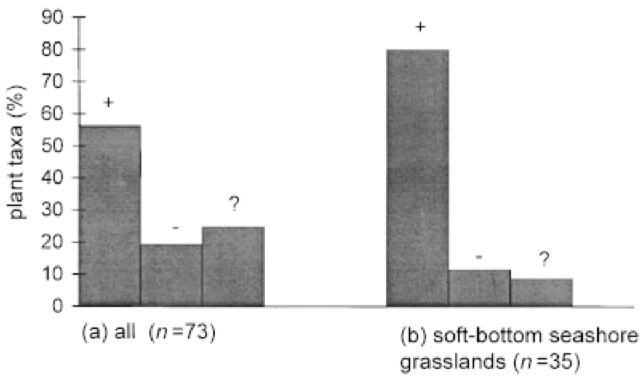

Figure 1. Effects of cattle grazing on Finnish vascular plant species and subspecies restricted to brackish shores of the Baltic Sea: (a) all taxa and (b) taxa of soft-bottom seashore grasslands. The figure shows the percentage of taxa benefiting (+) from or decreasing (−) because of cattle grazing. Question mark means the relationship is not known. Compiled from several sources (e.g., Kauppi 1967; Tyler 1969; Ericson & Wallentinus 1979; Bakker & Ruyter 1981; Härdtle 1984; Jensen 1985; Bakker 1989; Dijkema 1990; Ekstam & Forshed 1992; Jutila 1999).

Other Natural Disturbances

It is possible that traditional animal husbandry has also been a partial surrogate for several other important natural disturbances. Beavers, for example, were once an important ecosystem component. Beavers increase the area of herbaceous wetland vegetation a great deal (Coles & Orme 1983; Naiman et al. 1988). Some species possibly adapted to the beaver-made wetlands may have survived without beavers because of livestock grazing and mowing of the cleared wet forests. There are no empirical data yet, so research is clearly needed to support this hypothesis. Even though grasslands created by beavers differ from seminatural grasslands in many respects, they both create herbaceous vegetation.

Storm gaps in forests are probably important for the survival of many species (Peterken 1996). The opportunities for storms to create herbaceous vegetation in Europe have been suppressed by humans because trees are usually cut before they grow old. Even low-intensity, selective cutting of forests in the past decreased the density of uprooted trees, which caused shortages of exposed soil (Jonsson & Dynesius 1993). Gap species differ in their response to grazing and mowing, but I suggest that most of them have benefited from the opening of forests (semi-open forests and grasslands). Supposedly, many gap species have also benefited from traditional animal husbandry (Nilsson & Ericson 1997).

Traditional agriculture practitioners used plenty of wood, which affected biodiversity severely (Nilsson 1997). Nevertheless, pollarded deciduous trees (cut 1.5–3 m above the ground, with leaves used for winter fodder of animals) and constructions of untreated timber, such as barns and fences, were abundant and partially consisted of decaying wood and may have partially mitigated for the losses caused by wood usage. Pollarded trees are now the main habitat for many rare cryptogams and insects that are thought to be relics of the virgin forest (Rose 1992). There was probably more wood without bark in agricultural structures than in forests over large areas of Europe.

Interactions between Different Agents and Processes

The various biotic and abiotic agents and processes discussed separately above have several important interactions that may amplify their effects; these interactions are poorly understood. In beaver-made wetlands, for example, grazing by large herbivores may have been of great importance in suppression of tree growth. There were probably several important interactions between fires and indigenous large herbivores, although grazing reduces the frequency, extent, and intensity of fires (Hobbs 1996). Large herbivores prefer burned areas with nutrient-rich plant material (Daubenmire 1968). This co-evolution may explain why burning combined with grazing seems beneficial to many plant species (Green 1983).

Discussion

The differences and similarities of the effects of natural disturbances and traditional animal husbandry on ecosystems depend on their scale, intensity, timing, seasonality, and frequency. A variety of species and ecosystem responses can be expected when these variables change. Many natural disturbances are periodic, and whether continual disturbances such as grazing and mowing can replace natural disturbances is questionable. My hypothesis does not address the question of whether traditional animal husbandry can be used to replace natural disturbances (although there are similarities in ecosystem responses) but whether animal husbandry can further the survival of many species otherwise dependent on natural disturbances. In Northern and Central Europe, the abundance of trees is a key variable in terrestrial ecosystems. Both natural disturbances and traditional animal husbandry have created the treeless or semi-open habitats important to a large proportion of the European flora and fauna.

The prevalent use of European land for traditional animal husbandry had severe adverse effects on biodiversity: large areas were used relatively monotonously (although land use was more variable than today), and the amount of ancient woodland and dead wood decreased markedly (Ellenberg 1988; Nilsson 1997).

My findings do not emphasize the sole importance of traditional animal husbandry to the maintenance of biodiversity. They also emphasize that traditional livestock grazing and mowing have obscured our understanding of the importance of natural disturbance processes. The suppression of fire and other disturbances would probably have caused a more severe decline of biodiversity than expected, but this negative effect has been partly delayed by traditional agricultural management. Because considerable time may elapse before populations reach an equilibrium after habitat change (Tilman et al. 1994), it is possible that the occurrence and distribution of many species partly reflect past conditions. If neither natural disturbances nor traditional animal husbandry are revitalized, these species will disappear sooner or later.

Studies of the differences between traditional and modern agricultural management usually focus on the negative effects of plowing, seeding, and artificial fertilization. Besides fertilization, modern animal husbandry causes nutrient enrichment in several other ways. Animals are often given supplementary forages, or seminatural areas are fenced in with cultivated pastures, causing nutrient flow with animal feces from cultivated pastures to seminatural pastures (Londo 1990). Animals may be kept in seminatural pastures only at night. Because livestock graze mostly during the day and defecate at night, nutrient enrichment of seminatural pastures occurs. If grazing and mowing are used to maintain biodiversity, the nutrient capital in the area should be stable or declining (Bakker 1989; Marss 1993).

Freely moving livestock resemble more natural herbivore patterns than fenced livestock (Wallis de Vries 1995), partly because of the dispersal of plant propagules by freely moving livestock (Fischer et al. 1996). Large grazing areas usually include fertilized areas such as former arable fields, however, and the nutrient flow via the livestock may be from the arable land to the seminatural vegetation (Londo 1990). Theoretically, fenced livestock can also be used more precisely for managing biodiversity. Grazing is often considered more natural than mowing. Because of the lack of data, however, it is usually not possible to evaluate which method is better in compensating for the lack of specific natural disturbances in various ecosystems.

Some conclusions for nature conservation can be drawn. First, the optimal grazing management system for biodiversity is probably a complicated combination both of continuity (similar grazing pressure over a long time) and stochasticities (variation in grazing pressure, rotational grazing, and abandonment and resumption of grazing) and of different grazing pressures and animals over a variety of spatial and temporal scales. Second, when grazing and mowing are used for maintaining biodiversity, no human-induced nutrient supply (artificial fertilization, supplementary forage, nutrient flow via animal feces from cultivated pastures) should be allowed. This is a difficult goal to achieve because animal husbandry that does not cause nutrient enrichment is largely relegated to history. Nevertheless, this would be most important for maintaining biodiversity in the European agricultural landscape. The grazing system should be prescribed precisely to obtain relevant information on species' response to livestock grazing in different situations. Finally, the ideas I have presented suggest that further studies are urgently needed to clarify and verify the importance of traditional animal husbandry in compensating for the lack of natural processes in different ecosystems.

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Literature Cited

Anderson, P. 1995. Ecological restoration and creation: a review. Biological Journal of the Linnean Society **56(supplement):**187–211.

Andersson, L., and T. Appelqvist. 1990. Istidens stora växtätare utformade de nemorala och boreonemorala ekosystemen: en hypotes med konsekvenser för naturvården. (The influence of the Pleistocene megafauna on the nemoral and the boreonemoral ecosystems: a hypothesis with implications for nature conservation strategy). Svensk Botanisk Tidskrift **84:**355–368.

Bakker, J. P. 1989. Nature management by grazing and cutting. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Bakker, J. P., and J. C. Ruyter. 1981. Effects of five years of grazing on a salt-marsh vegetation. A study with sequential mapping. Vegetatio **44:**81–100.

Björk, S. 1967. Ecological investigations of *Phragmites communis.* Folia Limnologica Scandinavica **14:**1–248.

Bond, W. J., and B. W. van Wilgen. 1996. Fire and plants. Chapman and Hall, London.

Coles, J. M., and B. J. Orme. 1983. *Homo sapiens* or *Castor fiber*? Antiquity **17:**95–102.

Daubenmire, R. 1968. Ecology of fire in grasslands. Advances in Ecological Research **5:**209–266.

Demment, M. W., and P. J. van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. The American Naturalist **125:**641–672.

Dijkema, K. S. 1990. Salt and brackish marshes around the Baltic Sea and adjacent parts of the North Sea: their vegetation and management. Biological Conservation **51:**191–209.

Duffey, E., M. G. Morris, J. Sheail, L. K. Ward, D. A. Wells, and T. C. E. Wells. 1974. Grassland ecology and wildlife management. Chapman and Hall, London.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science **266:** 753–762.

Ekstam, U., and N. Forshed. 1992. Om hävden upphör: kärlväxter som indikatorarter i ängs- och hagmarker. (If grassland management ceases: vascular plants as indicator species in meadows and pastures). Naturvårdsverket, Solna, Sweden.

Ellenberg, H. 1988. Vegetation ecology of Central Europe. 4th edition. Cambridge University Press, Cambridge, United Kingdom.

Ellenberg, H. 1990. Eutrophication as a significant background problem. Pages 117–130 in M. F. Askew, editor. Agriculture. Rapeseed 00 and intoxication of wild animals. Commission of the European Communities, Directorate-General for Agriculture Coordination of Agricultural Research, Luxembourg.

Ellenberg, H., H. E. Weber, R. Düll, V. Wirth, W. Werner, and D. Paulissen. 1991. Zeigerwerte von Pflanzen in Mitteleuropa (Indicator values of plants in Central Europe). Scripta Geobotanica **18:**1–248.

Emanuelsson, U. 1988. A model describing the development of the cultural landscape. Pages 111–121 in H. H. Birks, H. J. B. Birks, P. E. Kaland, and D. Moe, editors. The cultural landscape: past, present and future. Cambridge University Press, Cambridge, United Kingdom.

Erhardt, A., and J. A. Thomas. 1991. Lepidoptera as indicators of change in the seminatural grasslands of lowland and upland Europe. Pages 213–236 in N. M. Collins and J. A. Thomas, editors. The conservation of insects and their habitats. Academic Press, London.

Ericson, L., and H. G. Wallentinus. 1979. Sea-shore vegetation around the Gulf of Bothnia. Wahlenbergia **5:**1–142.

Esseen, P.-A., B. Ehnström, L. Ericson, and K. Sjöberg. 1997. Boreal forests. Ecological Bulletins **46:**16–47.

Faliński, J. B. 1986. Vegetation dynamics in temperate lowland primeval forests: ecological studies in Bialowieza forest. Dr W. Junk Publishers, Dordrecht, The Netherlands.

Fischer, S. F., P. Poschlod, and B. Beinlich. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. Journal of Applied Ecology **33:**1206–1222.

Green, B. H. 1983. Management of herbaceous vegetation for wildlife conservation. Pages 91–116 in J. M. Way, editor. Management of vegetation. BCPC Publications, Croydon, United Kingdom.

Härdtle, W. 1984. Vegetationskundliche Untersuchungen in Salzwiesen der ostholsteininschen Ostseeküste. Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg **34:** 1–142.

Hillier, S. H., D. W. H. Walton, and D. A. Wells, editors. 1990. Calcareous grasslands. Ecology and management. Bluntisham Books, Bluntisham, United Kingdom.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management **60:**695–713.

Hodgson, J. G. 1987. Why do so few plant species exploit productive habitats? An investigation into cytology, plant strategies and abundance within a local flora. Functional Ecology **1:**243–250.

Hofmann, R. R. 1985. Digestive physiology of the deer: their morphological specialisation and adaptation. The Royal Society of New Zealand Bulletin **22:**393–407.

Hulme, P. E. 1996. Herbivory, plant regeneration, and species coexistence. Journal of Ecology **84:**609–615.

Janzen, D. H. 1982. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. Oikos **38:**150–156.

Jefferies, R. L., and J. L. Maron. 1997. The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. Trends in Ecology and Evolution **12:**74–78.

Jensen, A. 1985. The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. Vegetatio **60:**37–48.

Jonsson, B. G., and M. Dynesius. 1993. Uprooting in boreal spruce forests: long-term variation in disturbance rate. Canadian Journal of Forestry Research **23:**2383–2388.

Jutila, H. 1999. Effect of grazing on the vegetation of shore meadows along the Bothnian Sea, Finland. Plant Ecology **140:**77–88.

Kauppi, M. 1967. Über den Einfluss der Beweidung auf die Vegetation der Uferwiesen an der Bucht Liminganlahti im Nordteil des Bottnischen Meerbusens. Aquilo Ser. Botanica **6:**347–369.

Kirby, K. J., R. C. Thomas, R. S. Key, I. F. G. McLean, and N. Hodgetts. 1995. Pasture-woodland and its conservation in Britain. Biological Journal of the Linnean Society **56(supplement):**135–153.

Klemm, M. 1996. Man-made bee habitats in the anthropogenous landscape of central Europe: substitutes for threatened or destroyed riverine habitats? Pages 17–34 in A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, editors. The conservation of bees. Academic Press, London.

Kolev, Z. 1998. *Maculinea arion* (L.) in Finland: distribution, state of knowledge and conservation. Journal of Insect Conservation **2:**91–93.

Lennartsson, T., P. Nilsson, and J. Tuomi. 1998. Induction of overcompensation in the field gentian, Gentianella campestris. Ecology **79:** 1061–1072.

Londo, G. 1990. Conservation and management of semi-natural grasslands in Northwestern Europe. Pages 69–77 in V. Bohn and R. Neuhäusl, editors. Vegetation and flora of temperare zones. SPB Academic Publishing, The Hague, The Netherlands.

Marss, R. H. 1993. Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. Advances in Ecological Research **24:**241–300.

Martin, P. S., and R. G. Klein, editors. 1984. Quaternary extinctions; a prehistoric revolution. University of Arizona Press, Tucson.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience **38:**753–762.

Nilsson, S. G. 1997. Forests in the temperate-boreal transition: natural and man-made features. Ecological Bulletins **46:**61–71.

Nilsson, S. G., and L. Ericson. 1997. Conservation of plant and animal populations in theory and practice. Ecological Bulletins **46:**117–139.

Olff, H., F. W. M. Vera, J. Bokdam, E. S. Bakker, J. M. Gleichman, K. de Maeyer, and R. Smit. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. Plant Biology **1:**127–137.

Owen-Smith, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. Paleobiology **13:**351–362.

Peterken, G. F. 1996. Natural woodland: ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge, United Kingdom.

Puurman, E., and U. Ratas. 1995. Problems of conservation and management of the West Estonian seashore meadows. Pages 345–349 in M. G. Healy and J. P. Doody, editors. Directions in European coastal management. Samara Publishing Limited, Cardigan, United Kingdom.

Rackham, O. 1995. The history of the countryside. Weidenfeld and Nicolson, London.

Ridley, H. N. 1930. The dispersal of plants throughout the world. L. Reeve, Ashford, United Kingdom.

Rose, F. 1992. Temperate forest management: its effects on bryophyte and lichen floras and habitats. Pages 211–233 in J. W. Bates and A. M. Farmer, editors. Bryophytes and lichens in a changing environment. Clarendon Press, Oxford, United Kingdom.

Rundel, P. W. 1981. Fire as an ecological factor. Pages 501–538 in O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, editors. Encyclopedia of plant physiology. New series. Volume 12A. Physiological plant ecology. Springer-Verlag, Berlin.

Stoutjesdijk, P., and J. J. Barkman. 1992. Microclimate, vegetation and fauna. Opulus Press, Knivsta, Sweden.

Tamm, C. O. 1991. Nitrogen in terrestrial ecosystems. Springer-Verlag, Berlin.

Thomas, J. A. 1993. Holocene climate changes and warm man-made refugia may explain why a sixth of British butterflies possess unnatural early-successional habitats. Ecography **16:**278–284.

Thomas, J. A., D. J. Simcox, J. C. Wardlaw, G. W. Elmes, M. E. Hochberg, and R. T. Clarke 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. Journal of Insect Conservation **2:**39–46.

Thompson, K. 1994. Predicting the fate of temperate species in response to human disturbance and global change. Pages 61–76 in T. J. B. Boyle and C. E. B. Boyle, editors. Biodiversity, temperate ecosystems, and global change. Springer-Verlag, Berlin.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371:**65–66.

Tyler, G. 1969. Studies in the ecology of Baltic Sea shore meadows. II. Flora and vegetation. Opera Botanica **25:**1–101.

van Wieren, S. E. 1995. The potential role of large herbivores in nature conservation and extensive land use in Europe. Biological Journal of the Linnean Society **56(supplement):**11–23.

Verhoeven, J. T. A., W. Koerselman, and A. F. M. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology and Evolution **11:**494–497.

Vermeer, J. G., and J. H. J. Joosten. 1992. Conservation and management of bog and fen reserves in the Netherlands. Pages 433–478 in J. T. A. Verhoeven, editor. Fens and bogs in the Netherlands: vegetation, history, nutrient dynamics and conservation. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Wallis de Vries, M. F. 1995. Large herbivores and the design of large-scale nature reserves in Western Europe. Conservation Biology **9:** 25–33.

Wheeler, B. D. 1988. Species richness, species rarity and conservation evaluation of rich-fen vegetation in lowland England and Wales. Journal of Applied Ecology **25:**331–353.

Wheeler, B. D., S. C. Shaw, W. J. Fojt, and R. A. Robertson, editors. 1995. Restoration of temperate wetlands. Wiley, New York.

Whelan, R. J. 1995. The ecology of fire. Cambridge University Press, Cambridge, United Kingdom.

Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos **29:**22–32.