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Large herbivores: missing partners of western European light-demanding tree and shrub species?

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INTRODUCTION

The landscape of the temperate zone of western Europe has a long history of human occupation and impact. As the development of agriculture and the growth of the human population coincided with climate change since the last ice age, it is difficult to picture the landscape without human intervention. Based on palaeoecological data and reference sites, several authors state that temperate Europe without human influence would have been covered with a closed canopy broad-leaved forest in places where trees can grow (Ellenberg 1988, Peterken 1996). This perception is hereafter called 'the classical forest theory'. This forest type is thought to have regenerated by means of small or large gaps, or large windblown areas, where young trees could grow up. Indigenous species of large herbivores that lived within the range of this forest ecosystem are considered forest dwellers. In temperate Europe this applies to the Holocene aurochs (*Bos primigenius*), tarpan (*Equus przewalski gmelini*), red deer (*Cervus elaphus*), moose (*Alces alces*), roe deer (*Capreolus capreolus*) and European bison (*Bison bonasus*). The animals would not have had a substantial influence on the forest, but have followed the development in the vegetation (Tansley 1935, Iversen 1960, Whittaker 1977). The role of large herbivores in the broad-leaved forests is often discussed because the animals can prevent the regeneration of trees in the forest (see chapter 6 in this book). When large herbivores, such as deer,

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cattle and horses, are excluded from forests, this usually stimulates recruitment (Peterken & Tubbs 1965, Putman *et al.* 1989, Mountford *et al.* 1999). This has been used as an argument especially to exclude large ungulates like cattle and horses, because they are considered as an ‘unnatural’ component of forest ecosystems. Recent ecological and historical research on the role of these large herbivores in temperate wood-pastures (Vera 1997, 2000, Olff *et al.* 1999, Bakker *et al.* 2004), however, sheds doubt on the picture of the primaeval vegetation being a forest as well as on the view that large herbivores are not very important in temperate vegetation in its natural state. Wood-pasture ecosystems are found in places with a very long history of what is commonly considered as extensive livestock grazing. These are park-like landscapes grazed and browsed by livestock, like cattle and horses. They consist of a mosaic of grassland and thorny scrub thickets, with or without trees and forests (groves). Thorny shrubs mark the transition of the grassland to the forest, and form a so-called mantle and fringe vegetation (Watt 1924, Ellenberg 1988). Some authors consider wood-pastures as high forest, degraded by livestock because the animals prevented the regeneration of trees in the forest. As a consequence the forest became more and more open and transformed through so-called retrogressive succession into the park-like landscape that is characteristic of the wood-pasture (Moss 1913, Tansley 1953, Ellenberg 1988).

In this paper, we will discuss oak (pedunculate and sessile oak) and hazel in wood-pastures and forest reserves as a case study for trees with properties that may reflect adaptations to now-extinct large grazers, aurochs and tarpan. This discussion is important because it may yield that cattle and horses are to be key species in the ecology of temperate natural vegetation, in acting as ecological proxies for their extinct ancestors.

THE DISAPPEARANCE OF LIGHT-DEMANDING TREE AND SHRUB SPECIES

In central and western Europe many wood-pastures have been declared as forest reserves during the nineteenth and twentieth century. Cattle and horses were subsequently removed, because they were considered as alien species, introduced by man. Indigenous species like red deer, if present, were reduced to such low densities that they did not prevent the regeneration of trees in the forest. This caused wood-pastures to develop spontaneously into a closed-canopy high forest. These forests are then considered to be modern analogues of the primaeval vegetation (Falinski 1986, Peterken 1996).

In these forest reserves light-demanding woody species like pedunculate oak (*Quercus robur*), sessile oak (*Q. petraea*) and the shrub hazel (*Corylus avellana*) disappear. They are outcompeted by shade-tolerant species like beech (*Fagus sylvatica*), elm (*Ulmus glabra*) and *U. laevis*), hornbeam (*Carpinus betulus*), lime (*Tilia cordata* and *T. platyphyllos*), field maple (*Acer campestre*), sycamore (*A. pseudoplatanus*) and ash (*Fraxinus excelsior*) (Emborg *et al*. 1996, Vera 2000). Pollen analysis of both regional and local pollen rains, however, shows that both oak and hazel were very well represented in the primaeval vegetation in central and western Europe in the Atlantic period (8000–5000 BP). This is the period before the introduction of livestock when the primaeval forest is thought to have been optimally developed. In this period, the percentage of oak and hazel together in pollen diagrams varies between 20%–50% up to 60%–75% of the total pollen sum (Huntley & Birks 1983). This also shows that both taxa were present for thousands of years in the presence of shade-tolerant species. This raises the question whether the natural vegetation of temperate Europe was indeed a closed-canopy forest as is stated by the classical forest theory. Because the disappearance of these light-demanding taxa correlates with the removal and subsequent absence of the grazing large ungulates, cattle and horses, the question is raised whether these large herbivores may have maintained ecological conditions that are no longer present in the current forest reserves. Cattle and horses were in fact present in the primaeval vegetation by means of their wild progenitors, aurochs and tarpan (Söffner 1982, von Koeningswald 1983, Guintard & Tardy 1994), from which they are shaped in a process of domestication (Felius 1995). aurochs and tarpan went extinct in 1627 and 1887, respectively (Szafer 1968, Pruski 1963, Vereshchagin & Baryshnikov 1989). It is generally difficult to reconstruct ecological properties of species and ecosystems that do not exist anymore. However, the ecological properties of still existing tree and shrub species like oak and hazel can also tell us a lot about the prevailing ecological conditions in the past (Janzen & Martin 1982, Barlow 2000, Bakker *et al*. 2004).

OAK AND HAZEL IN FOREST RESERVES

As mentioned above, in the lowlands of Europe, wood-pastures became forest reserves over the last two centuries. This happened, for example, in the reserves: La Tillaie and Le Gros-Fouteau in the Forêt de Fontainebleau in France; the Hassbruch and the Neuenburger Urwald in Germany; the Dalby Söderskog in Sweden; the National Park Bialowieza in the Forest of

Bialowieza in Poland; and the Suserup Skov in Denmark (Emborg *et al.* 1996, Vera 2000). In these reserves, light-demanding oak, whether pedunculate oak or sessile oak, and hazel disappear and are replaced by shade-tolerant tree species like lime, beech, ash, elm, sycamore and hornbeam (Vera 2000). This also happened in parts of forests in the still existing wood-pasture of the New Forest, England, where cattle and horses were excluded by fences (Mountford *et al.* 1999, Mountford & Peterken 2003). Despite the presence of many seedlings on the forests floor, no new generations enter the older diameter classes, while the oldest classes that date from the time that cattle and horses grazed the area, disappear because of mortality. Oak does not regenerate successfully in small or large gaps. Only shade-tolerant species grow, inhibiting the oak seedlings (Vera 2000). Oak also fails to regenerate in large wind blown areas. These areas might act as a window of opportunity for the light demanding oak. However, shade-tolerant species having established a seedling bank under the closed-canopy, are released after a storm removed the canopy (Peltier *et al.* 1997, Houtzagers *et al.* 2000). The failure to regenerate results in a 'clock shaped' diameter distribution pattern of oak trees in these forest reserves (Fig. 7.1). This is a pattern that is typical for a population on the road to extinction (Christensen 1977). On the other hand, shade-tolerant species show a diameter distribution of an inverse J-curve. This means that many specimens of the younger age classes are present whereas the numbers decrease towards the older ages. This is considered as a sign of a successfully regenerating population. (Malmer *et al.* 1978, Lemée 1978, 1987, Emborg *et al.* 1996, Fig. 7.1).

Long-term spontaneous vegetation development in forest reserves also showed a strong decline in the cover of hazel (Malmer *et al.* 1978, Hytteborn 1986). This species disappears when it becomes overtopped by a closed canopy (Malmer *et al.* 1978, Hytteborn 1986, Peterken & Jones 1987).

COMPETITION FOR LIGHT IN A CLOSED CANOPY FOREST

Oak seedlings seem to be shade-tolerant because they grow well under low amounts of daylight in the first years of their lives (Jarvis 1964, Shaw 1974). However, the mechanism behind this phenomenon is not shade-tolerance, but rather a re-allocation of nutrients from the acorn into the taproot (Jarvis 1964, Brookes *et al.* 1980, Ziegehagen & Kausch 1995). Immediately after germination, seedlings of oak form an extremely extensive root system with a long taproot unparalleled by any other tree

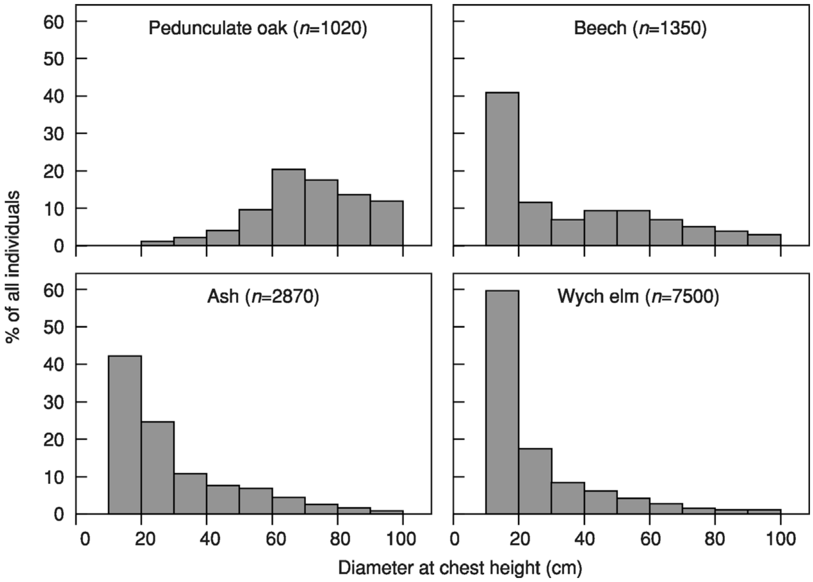

Figure 7.1. The percentage distribution per tree species in diameter categories per species of pedunculate oak, beech, ash and wych elm in Dalby Söderskog, Sweden. Only trees with a trunk diameter of >10 cm at chest height are included (redrawn from Malmer *et al.* 1978, from Vera 2000).

species in Europe (Jarvis 1964, Newbold & Goldsmith 1981, Van Hees 1997). If low amounts of daylight persist, the seedlings survive for some years on the nutrients in their taproots, but eventually die. Consequently, oak seedlings disappear from a forest within 3–5 years after germination (Watt 1919, Lemée 1987, 1992). Under similar amounts of reduced daylight, seedlings of shade-tolerant species like beech, lime, sycamore, field maple, wych elm *(Ulmus glabra)*, European white elm *(U. laevis)*, common elm *(U. minor/carpinifolia)* and ash persist for several to many years longer than oak (Vera 2000). Seedlings of beech, lime and hornbeam also show a morphological adaptation to conditions of low amounts of daylight. They have reduced height growth and form side branches. This gives them a wide shape (Pockberger 1963, Belostokov 1980, Suner & Röhrig 1980, Dupré *et al.* 1986, Pigott 1988), a greater leaf surface for catching the sparse daylight, and, therefore, a competitive advantage over oak seedlings.

The above mentioned characteristics give the shade-tolerant species the capability to establish a seedling bank under a closed-canopy. This pool of seedlings is released as soon as a gap in the canopy or a large windblown area is formed (Mayer & Tichy 1979, Raben 1980, Wolf 1982, 1988). The height growth of the shade-tolerant seedlings is fast, giving light-demanding young oaks virtually no chance (Eichhorn 1927, Bezacinsky 1971, Peltier *et al.* 1997). Sometimes, oaks do grow up in large gaps and remain ahead of beech in height growth for several years and up to a few decades (Von Lüpke 1982). None the less, eventually young oak becomes overgrown and out-competed by beech or other shade-tolerant species like lime, hornbeam, sycamore and elm (Bonnemann 1956a, b, Von Lüpke & Hauskeller-Bullerjahn 1999). Seedlings of Oak can only grow up successfully in the presence of seedlings of shade-tolerant species if the latter are constantly trimmed, as is done in forestry practice for with natural regeneration of oak (Vanselow 1926, Krahl-Urban 1959, Von Lüpke & Hauskeller-Bullerjahn 1999). Even mature oak are out-competed by shade-tolerant species if the soil properties allow these species to grow higher than mature oak (Bonnemann 1956a, b, Malmer *et al.* 1978, Ponge & Jean-Baptiste 1997).

Like oak, hazel re-allocates nutrients from the hazelnut into the taproot in the first growing season (Sanderson 1958). A reduction of daylight results in a clearly reduced development of the seedling. Under a closed canopy, hazel seedlings survive for not much longer than one year (Sanderson 1958, Vera 2000).

Altogether, these data show that in a closed-canopy forest, where regeneration of trees takes place in small or large gaps, or in large wind-blown areas, oak and hazel cannot persist in the presence of shade-tolerant tree species (Vera 2000).

REGENERATION OF OAK AND HAZEL IN WOOD-PASTURES

Contrary to the situation in closed-canopy forest, oak and hazel do regenerate very well in the presence of shade-tolerant tree species in wood-pastures that are grazed by large true grazers like cattle and horses (Watt 1919, Burrichter *et al.* 1980, Rackham 2003). They do so with densities of cattle, horses and deer as high as 110–130 and up to 187 kg ha^{-1} (Flower 1977, Putman 1986, Rackham 2003). Among these observations were densities of red deer of 30 animals per 100 ha (20 kg ha^{-1}) (Hart 1966, Vera 2000). These densities are far higher than 0.5 to 3 deer 100 ha^{-1} (0.4–3.2 kg ha^{-1}) that is usual for forests, as defined from the classical forest theory of a closed-canopy forest as climax vegetation (Wolfe & Von Berg 1988, Remmert 1991).

In wood-pastures, the seedlings of oak and hazel, as well as other tree and shrub species, establish in open grassland. In these grazed systems, such palatable seedlings can only survive there if they are close to or in the direct vicinity of shrub or herb species that have defences against large ungulates (Rousset & Lepart 1999, Vera 1997, 2000, Olff *et al.* 1999). Plant species with physical defences against herbivores are, for instance, blackthorn, hawthorn, juniper and brambles (*Rubus* spp.) that are 'armed by spines or thorns', while bracken (*Pteridium aquilinum*) and heather (*Calluna vulgaris*) are defended by chemical substances (Iason & Alison 1993, Mountford & Peterken 2003, Bakker *et al.* 2004). These species act as nurse species for palatable tree and shrub species. This defence of palatable species through spatial association is called associational resistance (Olff *et al.* 1999, Callaway *et al.* 2000, Milchunas & Noy-Meir 2002). In a recent study (Bakker *et al.* 2004), experimental evidence was found indicating that oaks do indeed need spiny shrubs (blackthorn) for their recruitment in grazed systems (Fig. 7.2). One-year-old seedlings of *Quercus robur* were planted in open grassland, between young spiny shrubs, in old

Figure 7.2. Effect of grazing on the survival of transplanted oak seedlings in different vegetation structure types in the Junner Koeland reserve, the Netherlands. Different letters indicate statistically different biomasses at the level $p<0.05$. From Bakker *et al.* (2004).

spiny shrub thickets and between large established oaks. In each vegetation structure, oaks were planted inside and outside exclosures, to separate low resource availability (light, nutrients) from herbivory as mortality causes. It was found that amongst young shrubs, the survival of the oaks was very high. In open grassland, recruitment failed because all oaks were grazed heavily. In the old thickets and under the established trees, establishment failed probably due to a combination of low light levels and grazing. The young shrub thickets provided protection while not being tall enough to out shade the seedlings. When the oaks then grow up, they out shade the plants that facilitated their survival (Watt 1934, Bakker et al. 2004, Fig. 7.3). Spiny species, however, are not absolutely defended against the large herbivores. Seedlings and new root suckers of blackthorn and seedlings of hawthorn, as well as young twigs of blackthorn and hawthorn are not spiny (Heukels & Van der Meijden 1983). The spines only harden at the end of the growing season. Therefore, young seedlings and the annual shoots of mature shrubs can be consumed by large herbivores (Buttenschøn & Buttenschøn 1978, Bokdam 1987). The browsing of annual shoots induces a dense canopy, that is almost impenetrable to the snouts of large herbivores. This enhances the protection of the undefended palatable tree and shrub species that grow in spatial association with the spiny species (Bakker *et al.* 2004). Unarmed seedlings, however, can rapidly disappear during their first growing season (Buttenschøn & Buttenschøn 1985, Mountford & Peterken 2003). On the other hand, both seedlings and mature shrubs can expand rapidly in open grassland when grazing pressure is reduced for a number of growing seasons, or if it suddenly stops altogether (Tansley 1922, Watt 1934, Smith 1980, Buttenschøn & Buttenschøn 1985).

Light-demanding shrub and tree species other than hazel and oak, that disappear in wood-pastures that have become forest reserves (Vera 2000), regenerate in wood-pastures through spatial association with spiny or thorny shrub species as well. Such shrub species are guelder rose (*Viburnum opulus*), wayfaring tree (*V. lantana*), dogwood (*Cornus sanguinea*), bird cherry (*Prunus padus*), spindle tree (*Euonymus europaeus*), elder (*Sambucus nigra*) and privet (*Ligustrum vulgare*). The tree species are wild cherry (*Prunus avium*), wild apple (*Malus sylvestris*), wild pear (*Pyrus communis*), rowan (*Sorbus aucuparia*), wild service tree (*S. torminalis*), whitebeam (*S. aria*) and true service tree (*S. domestica*) (Vera 2000). Several of them are nowadays endangered species (Dagenbach 1981, Rackham 2003). Besides hazel, all these shrub and tree species bear fruits eaten by birds (*Passeriformes*), which defecate the seeds below thorny shrubs (Namvar &

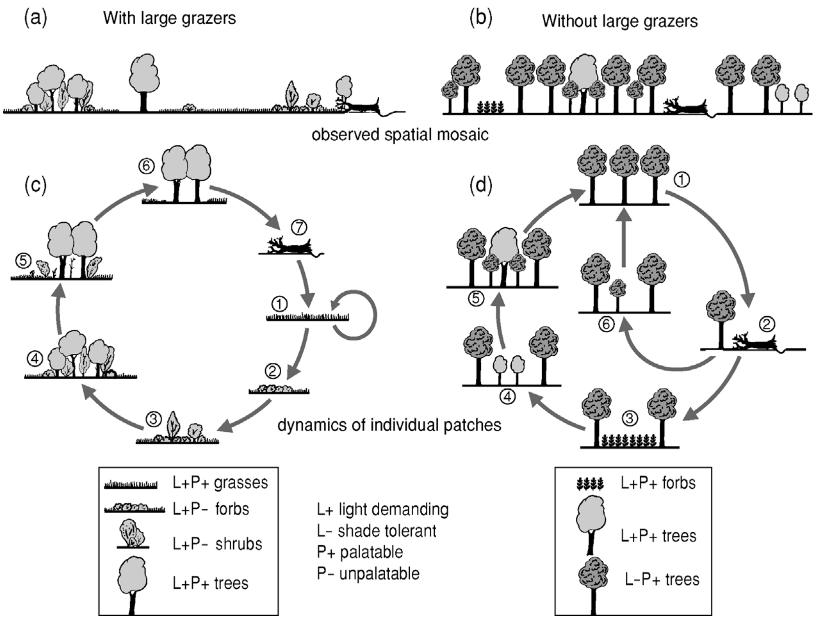

Figure 7.3. Observed spatial mosaic as mediated by local cyclical succesion of plant functional types in temperate woodlands (a) with and (b) without free-ranging large grazers, such as cattle and horses. Protection of palatable (P+) plant species by defended, spiny (P−) plant species is an important mechanism causing the dynamics of local cyclical succession in the presence of large grazers. This dynamics is therefore very different with (c) versus without (d) large herbivores. The differences are also caused by the interaction of palatability with light demand of the different woody species. Light-demanding trees and shrubs (L+) co-occur with grasses in the presence of large grazers. while shade tolerant trees (L−) dominate in the absence of large grazers. From Olff *et al.* (1999).

Spethmann 1985, Snow & Snow 1988). Shade-tolerant tree species also regenerate in wood-pasture in spatial association with thorny and spiny species (Tansley 1953, Hart 1966, Rackham 2003). A remarkable phenomenon is that compared to shade-tolerant tree species, oak (pedunculate and sessile oak) is very common in wood-pastures (Watt 1919, Pott & Hüppe 1991, Rackham 2003). This is caused by the activity of the jay (*Garrulus glandarius*).

THE JAY AND THE OAK

The jay (*Garrulus glandarius*) collects acorns and buries them from a few metres to up to several kilometres from the site of collection (Schuster

1950, Chettleburgh 1952, Bossema 1979). Schuster (1950) concluded that in 4 weeks, approximately 65 birds dispersed at least 500 000 acorns throughout the area. The jay performs a clear preference for open terrain (Kollmann & Schill 1996, Hauskeller-Bullerjahn *et al.* 2000, Stähr & Peters 2000) where they select short grass or the outer edge of hedges, the fringes of thorny scrub of blackthorn and the base of the stem of a thorny shrub like hawthorn or juniper (Bossema 1979, Vullmer & Hanstein 1995, Rousset & Lepard 1999). Shade-tolerant tree species lack a vector that plants their seeds in the direct vicinity of a nurse species. Compared to shade-tolerant tree species it seems that the jay gives oak an advantage in its establishment in wood-pastures. Mice also distribute acorns, but they do so over distances less than tens of metres (Jensen & Nielsen 1986, Rousset & Lepart 1999). Although mice hoard beechnuts as well, the infrequent appearance of beech seedlings and the frequent establishment of oak seedlings in grassland and thorny scrub near beech woods, shows that oak seems to have an advantage over beech (Tansley 1922, Watt 1925).

Hazelnuts have a vector as well, namely the Nuthatch *(Sitta europaea)*. This bird species plants hazelnuts (Sanderson 1958, F. W. M. Vera, personal observation 1995). The presence of hazel seedlings is limited to areas with open daylight like the thorny shrub species blackthorn and hawthorn, which are transitional area from forest to grassland, as well as open grasslands close to this transition. Because of this, hazel becomes part of mantle and fringe vegetation. It seems, however, that hazel is also able to persist in the presence of large ungulates without a nurse species (Bär 1914, Jahn 1991, Coppins *et al.* 2002).

THE FORMATION OF A PARK-LIKE LANDSCAPE

Blackthorn spreads clonally into open grassland and tree seedlings establish in the fringes of the advancing blackthorn. In this way, trees advance into the grassland at the same pace as the spreading fringes of the thorny scrub (Watt 1924, Pott & Hüppe 1991). Only rabbits can inhibit the clonal expansion of blackthorn (Bakker *et al.* 2004). Because blackthorn spreads from a nucleus in every direction, a characteristic convex shaped group of trees, called a grove can establish within the scrub (Vera 2000, Bakker *et al.* 2004). An expanding spiny mantle and fringe vegetation consisting of blackthorn and the associated seedlings, saplings and young trees that grow up in association with blackthorn surrounds the grove (Pott & Hüppe 1991, Vera 2000, Bakker *et al.* 2004). Inside the scrub itself the establishment of light-demanding as well as shade-tolerant trees is impossible because of the very low density of daylight (Dierschke 1974, Tubbs 1988), which may reach less than 2% of total daylight (Dierschke 1974). Light-demanding thorny nurse shrubs disappear from the grove because they are killed by shade cast by the crowns of trees they nursed that also shape the grove (Watt 1924, 1934, Ekstam & Sjögren 1973, Coops 1988). Regeneration of trees inside the grove is also limited due to grazing and trampling by large ungulates present in the wood-pastures (Mountford *et al.* 1999, Mountford & Peterken 2003, Bakker *et al.* 2004). Because the animals prevent the regeneration of trees within the grove, they prevent shade-tolerant species from growing up under oak and ousting it, as happens in forest reserves (Mountford & Peterken 2003). Because of the lack of regeneration within the grove, oak remains in the presence of shade-tolerant tree species and is part of the canopy of the grove. If a gap in the canopy of the grove is formed, the establishment of young trees is still prevented by the large herbivores. Fungi may facilitate the process of opening up the canopy and demise of the trees (Green 1992, Dobson & Crawley 1994) as well drought and storms (Mountford & Peterken 2003). Grasses, whose seeds often are brought in by large ungulates by means of their dung and fur, establish themselves and lawns are formed (Bokdam 2003, Mountford & Peterken 2003). As more trees die, the grove becomes more and more open, from the centre where the oldest trees stand onwards. In this way the grove changes gradually (degrades in the classical forest theory) from the centre into grassland (Goriup *et al.* 1991, Peterken 1996, Mountford *et al.* 1999, Mountford & Peterken 2003). This process is known as retrogressive succession in the 'classical forest theory' and has resulted in the large ungulates gaining the reputation of potential destroyers of the forest (Tansley 1911, Moss 1913, Ellenberg 1988). Light-demanding shrub species do not establish because there is still too much shade or the local grazing pressure is so high that the young seedlings of spiny species whose thorns are not yet hardened disappear (Mountford & Peterken 2003, Bakker *et al.* 2004). Tree species will not be able to establish, because they are not protected by thorny species. Only in the newly developed open grassland in the end, light-demanding thorny shrubs become established and again they protect young trees against the large herbivores. In this way a new grove can emerge from the grassland (Vera 1997, 2000, Olff *et al.* 1999).

Until now, it is not known what role ungulates like European bison, moose, red deer and horses may play in this process. Because they strip bark from trees and shrubs (Borowski & Kossak 1972, Falinski 1986), they may speed up the opening up of the grove.

The above-described process shows that large herbivores like cattle and horses facilitate the establishment of trees in open grassland and prevent the regeneration in closed-canopy forest. In fact they induce a non-linear succession, namely: grassland → thorny shrubs → grove → grassland → thorny shrub → grove, etc. This theory is called *the cyclic turnover of vegetation*. The resulting spatial shifting mosaic is very different from the mosaic in an ungrazed forest (Vera 1997, 2000, Olff *et al.* 1999, Fig. 7.3). Variations on this basal process are possible. The pattern of tree establishment may depend on the shrub species that nurse the tree and on the soil type. Blackthorn may lead to characteristic convex shaped groves, because the shrub reproduces vegetatively from a nucleus. Hawthorn on the other hand does not exhibit clonal vegetative reproduction and may nurse a solitary tree that will develop into an open grown tree. This will result in a more savanna like landscape. On more basic as well as more acidic soils bramble will nurse trees and on acidic soils holly (*Ilex aquifolium*), juniper or even old shrubs of heather will do so (Olff *et al.* 1999, Vera 2000, Bakker *et al.* 2004). Holly and juniper can also form low lying branches in between which the jay can plant several acorns. This results in small groups of oak in open vegetation. Bramble can nurse a similar or somewhat bigger group because of its ability to spread by runners. The shrub eventually becomes ousted by the shade cast by the open grown wide crowned trees.

The landscape may be more open in cases of very fertile soil because of the high densities of large ungulates that can occur on these soils. Seedlings of spiny species may have problems becoming established because their spines are formed at the end of the growing season and they may be grazed before that time. The Oostvaardersplassen in the Netherlands may be an illustration of this type of landscape. Without supplementary feeding the population densities of wild cattle, red deer and horses reach *c.* 1 animal 4 ha^{-1}, 1 animal 2 ha^{-1} and 1 animal 4 ha^{-1}, respectively, and hundreds of hectares of grassland remain open.

PROCESSES IN THE WOOD-PASTURE AS MODERN ANALOGUES OF FORMER RELATIONS?

If we compare forest reserves with wood-pastures, the forest reserves differ from the latter by the removal or absence of true grazers among the large herbivores. This results in the absence of light-demanding shrub and tree species. Although man introduced cattle and horses, he in fact replaced their two wild ancestral species, aurochs and tarpan, from which cattle and horses are derived by domestication. As far as their feeding strategies are concerned (Fig. 7.4), there is no difference between these domestic ungulates in the wood-pastures and their wild forms (Hofmann 1973, 1976, 1985, Van de Veen & Van Wieren 1980). Therefore, the processes that cattle and horses initiate in the wood-pasture can be considered as modern analogues of the former relationship between the vegetation and large ungulates. In conclusion, the wood-pasture is the closest modern analogue of the primaeval natural vegetation in areas where large ungulates like aurochs and tarpan lived.

A question that remains to be answered is whether the density of livestock in wood-pastures mimics those of their wild ancestors, or rather, were densities of wild ungulates in primaeval vegetation as high as the densities of livestock in wood-pastures?. There will not have been one overall density. Like in wood-pastures, there will have been differences because of the difference in accessibility and productivity because of soil fertility. However, the fossil records cannot answer the question about density because, first, the chance of fossilization depends on special conditions and is generally very small and, second, the chance of finding fossilized bones is very small (Davis 1987). What remains is indirect proof, like, for instance, the high proportion of pollen of oak and hazel in the pollen spectra, together with pollen of shade-tolerant tree species in periods when or areas where agriculture was absent (Vera 2000).

OTHER LINES OF EVIDENCE

There are other lines of evidence that support the theory that the uncultivated wilderness was a park-like landscape instead of a closed-canopy forest (Vera 2000). Lines of evidence are charters from the sixth century AD onwards, which regulated the use of the wilderness. These regulations concerned the fattening of pigs and the protection of so-called fruitful (light-demanding) trees such as oak, wild cherry, wild pear and crab apple that produced food (the mast) for pigs. The grazing of cattle and horses was regulated from the thirteenth century onwards in order to protect the re-sprouting stools of ‘hazel and thorn’, which were cut for firewood. The regulations ordered to spare the young trees that grew in between the thorny shrubs, like they do in the wood-pasture. Oak was particularly mentioned, because of its importance for the fattening of pigs and shipbuilding (Vera 2000). The places where this happened were indicated in

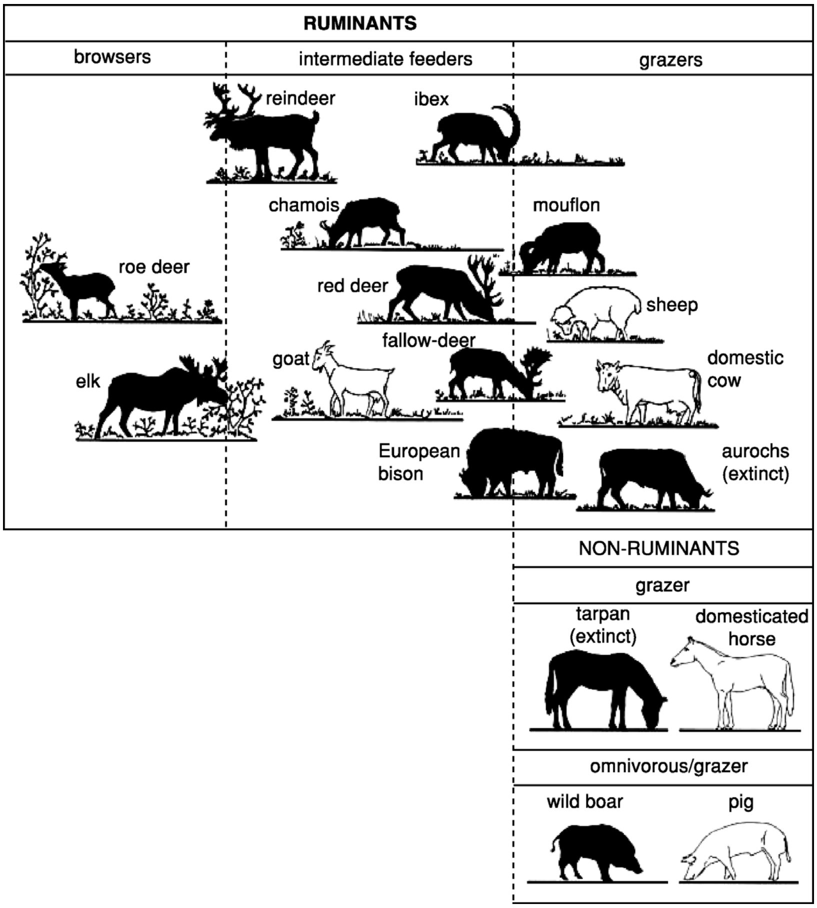

Figure 7.4. The different species of large herbivores indigenous in Europe, as well as the omnivorous wild boar, classified according to their feeding strategy. The domesticated species are shown in white. The indigenous species of the lowlands of central and western Europe include aurochs, tarpan, European bison, red deer, elk, roe deer and wild boar. (redrawn from Hofmann 1973, 1976, 1985, Van de Veen & Van Wieren 1980, from Vera, 2000).

charters with the terms ‘silva’, ‘forest’, ‘forêt’, ‘Forst’, ‘Wald’, ‘woud’, ‘bos’, ‘Busch’ and ‘wood’ in Latin, French, German, Saxon and Dutch. They did not mean forest or woodland in the modern sense of these words, but referred to places where there were trees with ‘wood’ as material as well as grassland and even treeless raised bogs (Vera 2000).

Other lines of evidence are pollen diagrams from areas from before the introduction of agriculture in the Holocene. The proportion of arboreal pollen (trees, including oak, and shrubs, including hazel) and non-arboreal pollen (grasses and forbs) from that period varies mostly between 90% and 95% arboreal pollen. The dominance of arboreal pollen is in the 'classical forest theory' interpreted as proof of the presence of a closed-canopy forest. However, pollen analyses of modern landscape show that such pollen diagrams can also be interpreted as park-like landscapes. For instance, an area with 30% open terrain with grasses and grains showed a percentage of non-arboreal pollen of 4.5% and 2.0%, respectively (Gaillard *et al.* 1998, Sugita *et al.* 1999). A closed zone of trees situated along the bank of a sampled lake (0.2 ha) surrounded by a landscape that consisted of more than 50% open cultivated land and of 30% semi-open land (20 to 50% tree coverage) in a radius up to 1000 m, showed a pollen image of 90% tree pollen (arboreal pollen) (Broström *et al.* 1998). All these data show that there is no linearity between the openness of a landscape and the percentage of non-arboreal pollen (Sugita *et al.* 1997, 1999, Gaillard *et al.* 1998). Besides these data, the high proportion of pollen of oak and hazel together varies from 20%–50% up to 60%–75% of the total pollen sum (Huntley & Birks 1983) is an important indication towards the park-like landscape (Vera 2000).

PRESERVING BIODIVERSITY

Because of the high variety of types of vegetation, wood-pastures have an extremely high diversity of plant and animal species (Harding & Rose 1986, Tubbs 1988, Rackham 2003). Bulk grazers like cattle and horses are key elements in the processes that are responsible for this high diversity (Vera 2000). The oak itself has a special place as a host for insects. There is no other species of tree in Europe associated with so many species of insects (Darlington 1974, Morris 1974). More than 50% of all the species of insects found in the whole of Great Britain live in the wood-pasture of the New Forest alone (20 000 hectares) (Tubbs 1988, Alexander 1998). Of all the European species of butterflies, 80% live in a habitat combining grasslands, scrub and groves with mantle vegetation (Bink 1992). Furthermore, there is an enormous variety of species of birds, especially songbirds (Smith 1980, Hondong *et al.* 1993, Cramp 1988, 1992).

SUMMING UP THE VIEWPOINTS

The disappearance of oak and hazel and other light-demanding species in the forest reserves shows that oak and hazel reflect past environmental adaptations that no longer exist in these reserves. In forest reserves these species as well as other light-demanding species are ecological anachronisms. The presence and the successful regeneration in wood-pastures of light-demanding tree and shrub species shows that the environmental conditions these species require are still there. The large ungulates cattle and horses play a key role in the processes of creating these environmental conditions. Being modern analogues of aurochs and tarpan, cattle and horses highlight that in wood-pastures light-demanding oak and hazel and other light-demanding tree and shrub species, reflect adaptations of the now-extinct grazers aurochs and tarpan.

In wood-pastures the natural interplay of herbivores and plant defences is still at work. The evolution of spiny and thorny shrub species that protect palatable tree and shrub species through associational resistance may have been enforced by large herbivores (Milewski *et al.* 1991). The presence of these taxa as well as large ungulates goes back through the Pleistocene to as far as the Tertiary (Tallis 1991, Agusti & Anton 2002). They lived together for millions of years. It is striking that the current ecological distribution of woody species with thorns and spines in the Netherlands coincides with the preferred distribution of large herbivores in grazed landscapes, namely on dry, fertile soils.

In conclusion, the wood-pasture can be considered as the closest modern analogue of the primaeval natural vegetation in situations where large ungulates lived (Vera 1997, 2000). Contrary to the classic forest theory, the wood-pasture system can explain the presence of light-demanding as well as shade-tolerant species in the primaeval vegetation, together with the presence of large grazing ungulates. Our study provides an interesting case showing that current ecological traits of species can tell us something about their ecological context in the past – which can have important lessons for current conservation strategies.

THE THEORY IN A BROADER PERSPECTIVE

This is not the only theory about a key role for large herbivores with regard to the structure and species composition of the natural vegetation. It is suggested that in Beringia, the Pleistocene mega fauna played a key role in maintaining grass-dominated steppe conditions, and that the disappearance of these animals at the end of the Pleistocene, probably because of the hunting pressure by anatomically modern people, caused a shift of grass-dominated steppe to moss dominated tundra, irrespective of climatic change (Zimov *et al.* 1995).

The theory of wood-pasture as the nearest modern analogue of primaeval vegetation has been commented on and criticized by several authors (Svenning 2002, Bradshaw *et al.* 2003, Rackham 2003, Whitehouse & Smith 2004). In a review of palaeoecological data Svenning (2002) states that a closed forest would predominate in so-called normal upland situations, but includes localized longer-lasting openings. Open vegetation would have been frequent on floodplains, infertile soils, chalklands and in continental and sub-Mediterranean areas. Large herbivores and fire would have been potential key factors in creating open vegetation in northwestern Europe.

Svenning (2002) states that the low percentage of non-arboreal pollen can indeed be interpreted as proof for the presence of a closed canopy forest, because among fossil beetles there is a similar low percentage of species connected with vegetation openness. He then concludes that, therefore, oak and hazel can persist in a closed-canopy deciduous species-rich forest. Data from the large island Zealand in Denmark would support his conclusion. Aurochs and moose would have become extinct there 7000–8000 years BP, because no fossils are found afterwards (Aaris-Sørensen 1980). Oak and hazel remained there during the mid-Holocene (6200–5200 BP) with shade-tolerant species like lime, ash and sycamore. Therefore oak and hazel occurred in a species-rich forest with shade-tolerant species even in the absence of large grazers.

This interpretation disregards the facts revealed by the developments in forest reserves. One of them is on the island Zealand itself. It is called Suserup Skov and is a former wood-pasture (Fritzbørger & Emborg 1996). It was protected in 1854. There are oaks of 250 to 500 years old and many have wide crowns and short boles, showing they grew up in open conditions. Nowadays it is a closed-canopy forest where oak and hazel are replaced by shade-tolerant species like lime, ash, sycamore, beech and hornbeam (Emborg *et al.* 1996), of which the first three taxa were present during the mid-Holocene together with oak and hazel (Hannon *et al.* 2000). Concerning the absence of grazers on the island of Zealand, it should be stressed that one of the basic rules in palaeoecology is that absence of proof is no proof of absence (Davis 1987).

The data concerning beetles used by Svenning (2002) are according to Whitehouse & Smith (2004) less convincing. The percentages of open area taxa, routinely presented by palaeoentomologists, reflect abundance within the sample and do not indicate *direct proportions of associated habitat* (italics by Whitehouse & Smith 2004). Although she states that using fossil beetles to examine openness has potential, it is presently not possible to estimate percentages of landscape openness/closeness from beetle records. The interpretations have been largely intuitive (Dinnin & Sadler 1999, Whitehouse & Smith 2004).

Svenning (2002) as well as Whitehouse and Smith (2004) refer to fire as an important disturbance agency. Especially in the eastern United States, fire received much attention in relation to the failure of oak to regenerate in closed-canopy forests (Abrams 1992, 2003, Frelich & Reich 2002). Here there are about 30 species of oak (Abrams 1996), almost all of which are light-demanding (Smith 1993, Dey 2002). As in Europe light-demanding oak species do not regenerate successfully in forest reserves, either in small or large gaps. They are replaced by shade-tolerant species like american beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), silver maple (*A. saccharinum*), red maple (*A. rubrum*), basswood (*Tilia Americana*), white ash (*Fraxinus Americana*) and American elm (*Ulmus Americana*). Also the light-demanding fast growing yellow poplar (*Liriodendron tulipifera*) that can, like oak, be long lived, can suppress oak (Peterken 1996, Brose *et al.* 1999, McCarthy *et al.* 2001). Even in large wind blown areas created by catastrophic storms, only shade-tolerant species are released (Spurr 1956, Hibbs 1983, Peterson & Picket 1995). Such events actually speed up the replacement of oak (Nowacki & Abrams 1992). Oak only regenerates in circumstances where the shade-tolerant species cannot thrive like xeric conditions (McCune & Cottam 1985, Orwig & Abrams 1994, Frelich & Reich 2002). According to pollen diagrams, oak, however, survived next to shade-tolerant taxa such as *Tilia, Acer, Fagus, Ulmus* and *Fraxinus*. The percentage of pollen from oak forms a much larger portion of the pollen diagrams than in Europe, namely from 40 to up to 70% (Watts 1979, Delcourt & Delcourt 1991, Clark 1997).

According to Abrams (1992, 2002, 2003), the successional replacement of oak by shade-tolerant species is caused by the suppression of wildfires, that started around the 1930s. He formulated the so-called fire and oak hypothesis (Abrams 2002). According to this hypothesis, fire eliminated the regeneration of shade-tolerant species. Fire also created open landscape that would be necessary for the light-demanding oak to survive. He refers to historical descriptions of the east of the United States, indicating the presence of open, park-like landscapes with open forests and areas where forests alternated regularly with grasslands (Cronon 1983, Whitney & Davis 1986, Covington & Moore 1994). The burning by Native Americans would have created this open park-like landscape. Therefore, fire could explain why oak continued to exist in the presence of shade-tolerant species like maple, lime, beech and ash for thousands of years (Abrams & Seischab 1997).

There is doubt about the evidence for large-scale burning of forests by Native Americans (Day 1953, Russell 1983). Russell (1983) states that the openness of the landscape in itself is used as the evidence of large-scale burning. Because there were open forests everywhere, there must have been burning everywhere, because otherwise the phenomenon cannot be explained. Several authors (Whitney & Davis 1986, Huddle & Pallardy 1996, Arthur *et al.* 1998) also pointed out that fire is not as selective with respect to oak as is assumed. Therefore, it is not clear at all whether oak species, for instance white oak (*Quercus alba*), do benefit from fire. This species is the most widely distributed light-demanding oak species in the eastern United States and a common species before European colonization in so-called presettlement forests. White oaks, 300–500 years old, became established in a period without clear traces of fire. Even during a recent historic fire regime no successful regeneration took place (McCarthy *et al.* 2001).

Abrams (2002, 2003) considered the presence of charcoal to be an indication of the role of fire in prehistoric times. However, from analyses of pollen and charcoal in sediments, it appears that fire cannot have played the role in forests in the eastern United States that has been ascribed to it (Clark 1997, Clark & Royall 1995, Clark *et al.* 1996). In most of the east of the United States, oak appears to have maintained itself in the company of shade-tolerant genera in more moist regions on soils with good moisture levels for thousands of years without clear palaeoevidence of fire. Therefore, other factors must have allowed the subsistence of oak in the long-term in the absence of fire (Clark 1997). It cannot have been catastrophic storms, because as mentioned earlier, only shade-tolerant species will be released. Therefore, as Frelich and Reich (2002) stated, in the absence of fire the mechanism for the establishment of oaks within the mesic forests dominated by shade-tolerant species remains a mystery.

However, the development of closed-canopy forests in the east of the United States did not only take place in the absence of fire. As in Europe, large grazing ungulates were absent as well. However, in the eastern United States prior to the early nineteenth century, the large grazer bison (*Bison bison*) was present (Vera 2000). At the time of colonization by the Europeans large numbers were there (Smith 1962, McHugh 1972, Joke & Sawtelle 1985, cited in Crow *et al.* 1994). They left traces in the landscape, as is shown by the first railroads that were constructed through the Appalachians from the east in a westerly direction that were laid on bison trails (Smith 1962, McHugh 1972). For example, around 1770 more than 10 000 bison were present in North Pennsylvania. The bison disappeared soon after colonization of the east of the United States. In North

Pennsylvania none were left 70 years later in 1840 (McHugh 1972, Day 1989). In 1825, the bison was extinct in West Virginia (Day 1989).

Being a specialized grazer, the influence of the bison in the eastern United States could have been analogous to specialized grazers like cattle and horses in Europe. Trees would have regenerated in open grassland with thorny bushes as nurse species, while groves would have changed into grassland. There are more than 30 species of hawthorn in the eastern United States, most of which are thorny (Britton & Brown 1947). This process could explain the permanent presence of open, park-like landscapes known from the historical descriptions, without the presence of fire. In the eastern United States oak does regenerate in thorny bushes in grassland grazed by cattle (Scot 1915, Marks 1942). It is striking that in Ohio where there was heavy grazing by cattle until 1940, white oak was present in all year classes (Whitney & Somerlot 1985). Concerning the role of fire in the regeneration of oak, it should be kept in mind that fire has been proposed as a disturbance agency within the framework of the natural vegetation being a closed-canopy forest. This framework implied that large grazers would not have had a substantial influence on the forest and followed the development in the vegetation. Our study of oak in the eastern United States indicates that the answer to the question posed by Abrams and Seischab (1997): 'What disturbance factor other than fire could historically have prevented these species from replacing oak?', may be large grazers like bison. Burning by Native Americans would then have made the landscape more open than it already was.

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