BSc Biology

On the debate of vegetation openness of primeval north-western Europe

Paleoecology and mechanisms

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Abstract

Since a few years a debate has been going on over what the primeval vegetation structure of north-western Europe looked like. From the beginning of the Holocene to the start of large agricultural activities the influence of humans on the structure vegetation was minimal compared to today. The question is whether without this influence by humans, would the landscape consist of closed canopy forest or would it be of a more open structure. Frans Vera has theorized that under influence of large grazers the landscape was of a half-open and dynamic structure. Many researchers, mainly paleoecologists, have called this to question however and used a wide variety of studies to get the answers. Studies on mechanisms and processes that are at work in forest ecosystems are important in furthering the debate since they can tell us how half-open landscapes. Today's equivalent of Vera's half-open landscape are which consist of alternating grasslands and groves, small groups of trees. Abiotic disturbances such as wind, floods and fire are some that have been known to influence forest structure. Biotic disturbances, such as grazers are also important since they have been shown to retard the rejuvenation of trees. Tree seedlings can however be protected by the process of associational resistance. Since grazing intensity is controllable by men, we can influence today's nature reserves naturally. But recreating past conditions is not always possible due to the fact that past plant and animal species are extinct. Furthermore grazing intensity by large grazers of the past is difficult to assess. At present the debate is still ongoing, and new insights are needed to resolve it.

Contents

Introduction

The influence of mankind on its environment has been substantial since prehistoric times (Weisman 2007). This influence has greatly increased ever since they converted lands for agricultural use. In north-western Europe these significant changes in the landscape brought about by humans are thought to have started around 5000 BP (before present) during the time when agriculture was introduced in this area (Vera 2000). For over 50 years there had been a general consensus regarding how the primeval landscape of north-western Europe looked before the onset of major anthropogenic change (Birks 2005). Most of the mixed deciduous forest that is left undisturbed by humans in north-western Europe today is of closed structure (Bradshaw et al. 2003). Furthermore, historical research on succession of vegetation suggested that any piece of bare ground will be colonized by seedlings of herbs and trees and eventually grow out to a closed forest after several successional stages (Vera 2000). When only taking these points into account one might conclude that the primeval landscape of north-west Europe primarily consisted of closed canopy forest; this is sometimes referred to as the 'classical succession theory' (Yamamoto 2000).

Recently however an intense debate began over whether the present-natural vegetation in north-western Europe would be closed forest (Mitchell 2005; Svenning 2002). The hypothesis that the primeval landscape of this region consisted mainly of closed canopy forest has recently been challenged by Frans Vera (Vera 1997; Vera 2000). He proposes that large herbivores, namely tarpan, aurochs and deer, were an important factor in giving the primeval landscape of north-western Europe its shape. He suggests that these large herbivores, consisting of deer, bison, aurochs and tarpan (wild horse), determined and controlled primeval forest structure and composition to a high degree. This is in stark contrast to the closed forest hypothesis which implies that the forest structure controls the population size of these animals and not the other way around. Vera compares this system with today's wood pastures which consist of alternating grasslands and groves, small groups of trees, which are being grazed upon by today's equivalent of past large grazers: horses and cattle (Bakker et al. 2004). Thus two conflicting hypotheses exist on the structure and composition of the primeval landscape of north-western Europe

and the role of large herbivores and other disturbances in temperate forests in this region. The outcome of the debate is an important one since Vera's theory has already been known to influence discussions on nature conservation policy (Kirby 2004).

So what was the structure of the landscape of primeval north-western Europe? In this thesis I try to summarize and commentate on the ongoing debate that revolves around this question using the field of paleoecology and studies on natural occurring mechanisms. In the end of this thesis I try to conclude the most likely outcome of the debate and in what fields of study further research is needed to find answers in the debate stimulated by Vera's theory.

In the first chapter the field of paleoecology is introduced and I explain why this field has been important in the debate. Paleoecological studies provide data against which the conflicting hypotheses can be tested (Svenning 2002). Much has been written about the natural history of temperate forests and many modern studies on it are at least partly based on paleoecological research. Iversen, one of the first scientists to use paleoecology as his primary base of study, postulated an important theory in 1941. With it he showed that a sharp decline in tree pollen could be seen in pollen diagrams indicating large scale clearance of tree species in a short time. This sharp decrease is dated at about 5000 BP. Iversen assumed in his theory that before this time a closed forest dominated the landscape. Many pollen studies have since been undertaken to study the openness of vegetation structure before this event occurred (Fyfe 2007).

In the following chapter I will describe different mechanisms at work in half-open landscape ecosystems. To understand how these half-open landscapes that Vera describes can arise and be sustained it is important to understand the ecological mechanisms at work in forest ecosystems. Disturbances such as grazing, fire, flooding can have great impacts on the vegetation composition in these ecosystems through there influence on competition and facilitation between plant species. The theories on succession formulate that any piece of bare ground will develop a particular vegetation composition through a number of successive stages (Vera 2000). Disturbances of the structure of the vegetation can influence this process making the dynamics of these ecosystems less predictable (Bradshaw et al. 2005).

In the final chapter I will discuss the debate and make my final conclusions. Different management types for near natural forest systems in Europe are under debate (Soepboer & Lotter 2009). If Vera's theory proofs to be valid, then nature conservation policies across Europe are often mistakenly implementing conservation actions that benefit closed forests if their actual aim is to reconstruct a landscape close to its natural condition prior to large human impact (Mitchell 2005). If this primeval landscape was of half-open structure due to the presence of large herbivores at may be that today's recruitment strategy of woody species is an adaption to these grazers that are now extinct. However this co-evolution continued after the primeval grazers went extinct. And they even continue today since proxies of these grazers exist in the form of today's domesticated horse and cattle (Bakker et al. 2004). These grazers have roughly the same function in the system, especially the tarpan and aurochs, so introducing them as free-range grazers in certain environments where large grazers were naturally present in the past recreates a part of the system. The introduction of the grazers is not only a step in the direction of self-regulation of these systems (due to the co-evolution), but it also promotes structural heterogeneity creating more niches. Both these effects of reconstructing past systems can increase biodiversity of that area (Bakker et al. 2004).

Therefore the question whether primeval forests were closed or (half) open is in my eyes an important one.

I: Paleoecology

Paleoecology is the study of ecology in the past. Using a variety of techniques it reconstructs the composition of species in a region in a certain time period. It has been recognized since the 19th century that this kind of reconstruction can give us a better understanding of past ecosystems than when looking at a single fossil of species of animal (Bradshaw & Mitchell 1999). In general the further back in time this reconstruction goes, the less accurate it is and the more uncertainty exists. The paleoecological data of the period between the end of the last glacial and the present interglacial is however fairly complete since micro and macrofossils have been relatively well preserved (Bradshaw & Mitchell 1999).

Palynology and other proxies

Within the science of paleoecology, palynology, the study of microfossils including pollen, spores and seeds, has been a major discipline since the early 20th century. Use of pollen as paleoecological proxies dates back to 1916. The Swedish geologist Von Post created pollen diagrams from which the vegetation composition of the landscape could be reconstructed (Vera 2000). This tool has been used ever since and enables us to not only build a model of the life environment of the fossils found but also visualizes the past climatic changes since these changes directly influenced vegetation composition.

Many inaccuracies and inconsistencies can be present using paleoecological tools which can cause a biased picture of past vegetation composition. For example, certain pollen degrades faster than others and certain plant species have larger amount of pollen than others. Both of these factors can contribute to a disproportional amount of pollen recorded for certain plant species causing these to be overrepresented in the diagram. Furthermore, pollen cores are generally taken from deposits where the pollen is well preserved. These include humid habitats like peat bogs, lake shores and even former lakes. Since these places have particular environmental conditions sampling from them can influence the relative frequency of pollen from certain plant groups such as water plants, compared to pollen from the surrounding region which have to travel a longer distance and are therefore selected (Vera 2000; Birks 2005).

However if the data derived from the pollen core is of good quality it can be used to determine generalised abundances of the plant species that were present at the time the layer was deposited (see figure 1). While not as precise as standard vegetation inventories, they are far better than presence/absence data (Bradshaw & Mitchell 1999). Other paleoecological proxies can of course magnify the precision when determining the age of the layers of the soil. Charcoal layers for example are indications of natural or unnatural (human-induced) fire (Bos et al. 2005) (see figure 1). Radiometric dating and dendrology are among the other tools that can be used to determine the age of wood fossils. Thanks to these tools pollen diagrams can be accompanied by time scales giving a clearer picture of the evolutionary changes in the composition and structure of vegetation.

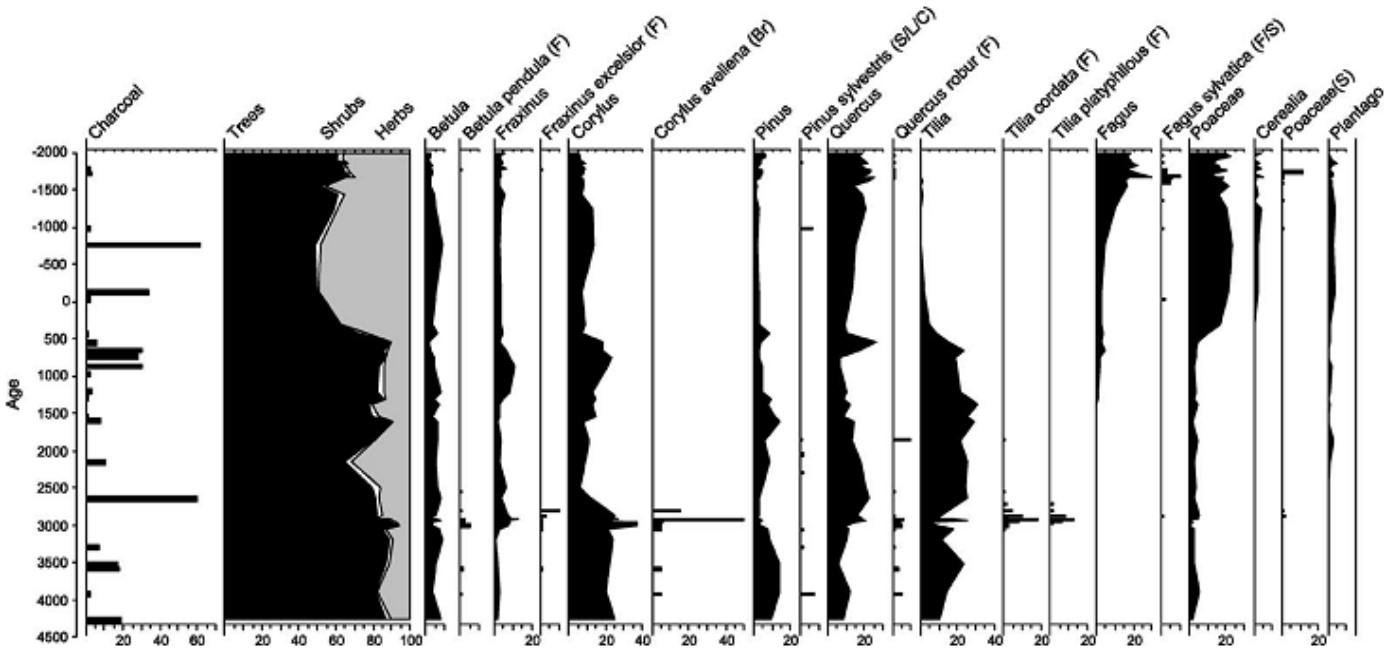

Figure 1 A pollen (continuous curves) and macrofossil (histogram) diagram from a small hollow in Denmark. Pollen curves are percentages of terrestial pollen sum and macrofossils are number of specifmens/ 50 ml of sediment. The charcoal data are numbers of fragments >200 mm/ml sediment. Macrofossil abbreviations are: F, fruit; Br, bract; S, seed; L, leaf; C, cone. The abundance of Quercus and Corylus between 4000 and 500 BC indicates that there were openings in the forest. Source: Bradshaw et al. (2003)

BOX: Paleoecological history since the last ice age

During the last 2.6 million years in the Pleistocene and Holocene, together known as the Quaternary, the climate of north-western Europe has been going through a cyclical variation consisting of glacial and interglacial periods. These climatic patterns are caused by variations in the earth's orbital eccentricity, obliquity, and precession, all external factors collectively known as the Milankovitch cycles. This is because the amount and location of solar radiation reaching the earth's surface depends on the combined effect of these factors.

The composition and structure of vegetation in Europe in the Quaternary was and is primarily driven by this variation in climatic conditions. Consequentially it not only influenced the vegetation but with it the presence and distribution of other organisms including animals. In Europe the last of the glacial periods is called the Weichsalian in the north-west or Devensian on the British Isles and lasted until approximately 10,000 BP when the current interglacial, the Holocene, began.

Before this time great changes in the composition of plant species across Europe had already been underway due to a climate shift. After the Last Glacial Maximum (LGM) in the last ice age, about 18,000 BP, the average temperature had slowly gone up. After the ice age ended approximately 14,000 BP plant species began to emerge from their refugia into which they had been forced due to the dry and cold conditions (Willes & Whittaker 2000).

In the Holocene temperatures rose across Europe influencing the vegetation and landscape. The glaciers covering the north melted leaving geological scars on the landscape. And in the following millennia, the species of vegetation that were pushed into their refugia by the climatic conditions of the ice age slowly spread back over Europe. These refugia were located in southern and south-eastern Europe in regions that had been relatively warm during the ice age (see figure 2). Woody plant species began to establish into north-western Europe beginning with the birch (*Betula* sp.). The climatic shifts from cold and dry during the Weichsalian to warmer and wetter conditions in the beginning of the Holocene have been well documented by paleoecological studies.

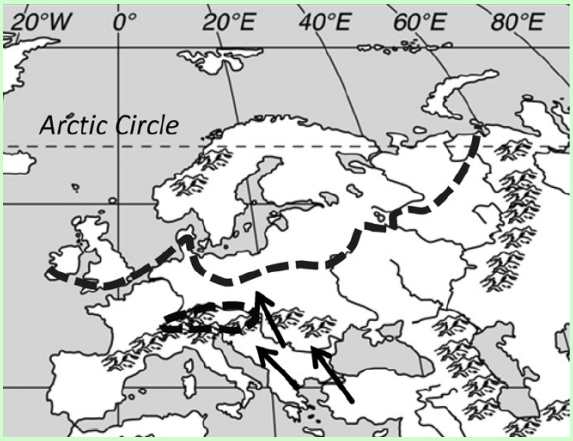

Figure 2 Map of Europe showing the southern limit of the last ice age (dashed line) and the migration routes of woody plant species out of their refugia following the last ice age (arrows). Source: Lev-Yadun & Holopainen (2009).

Iversens landnam

The start of large agricultural activities in north-western Europe is clearly seen in the paleoecological record. Cultivation of land for the growth of cereals started in the Middle-East around 10000 BP. By 5500 BP, these developments had reached north-western Europe. This so called Neolithic Revolution was the transition from hunter-gathering societies to agricultural based settlements. In the palynological records a sharp decrease in tree pollen and the first sighting of cereal pollen is seen in one pollen zone. This pollen zone is generally dated as being on the boundary of the Atlantic and Sub-Boreal period (see Table 1). In 1941 Iversen concluded that in this pollen zone, which he observed in Denmark, a sharp decline in relative frequency of arboreal (tree) pollen could be seen. He realized that his discovery matched with archaeological findings that pointed out that the agricultural revolution had reached this region (Vera 2000). Iversen called this the landnam, which is an Old Norse and Danish word for 'taking land' and the pollen zone corresponding to this event is now often called landnam as well.

Table 1 Pollen zones and their respected paleoecological and archaeological periods and dominant vegetation. Dates are approximate and from several sources and are in calibrated carbon years. Sources: Vera (2000), Iversen (1964; 1973)

Zone	Archaeological periods	Dates	Dominant vegetation type
IX	Iron Age to present	2500 BP - present	Grasslands
VIII	Neolithic and Bronze age	5000 – 2500 BP	Mixed deciduous forest
Landnam	Neolithic Revolution	ca. 5000 BP	Mixed deciduous forest
VII	Mesolithic	8000 – 5000 BP	Coniferous and mixed deciduous forest
V and VI	Mesolithic	9000 – 8000 BP	Pine and birch forest
IV	Late Upper Paleolithic and early - mid Mesolithic	10,000 – 9500 BP	Birch forest
III	Upper Palaeolithic	11,000 – 10,000 BP	Tundra
II	Upper Palaeolithic	11,700 – 11,000 BP	Tundra – mixed forest
Ic	Upper Palaeolithic	14,000-13,700 BP	Tundra
Ib	Upper Palaeolithic	14,700-14,000 BP	First tree species appear – Tundra
Ia	Upper Paleolithic	19,000 – 14,700 BP	Last Glacial Maximum - Tundra

The pollen zones below the landnam pollen zone show a constant dominance of tree pollen. Percentages of non-arboreal pollen (NAP) of below 10% have generally been interpreted as evidence for a closed forest (Svenning 2002). So did Iversen, when he concluded from his own pollen diagrams that before the landnam north-western Europe had been a closed forest (Vera 2000). His diagrams showed this closed forest as a mixed oak tree forest and the sharp decline of tree pollen was mostly due to the relatively decrease in elm (*Ulmus* sp.). In his landnam pollen zone Iversen also found the first presence of two species of herbs, greater plantain (*Plantago major*) and narrow-leaved plantain (*Plantago lanceolata*) that are generally considered to be indicators of agricultural activity (Vera 2000). Since these first farmers appeared, agriculture has forever changed the north-western Europe landscape (Rowley-Conwy 2004).

These first farmers, often called "primitive agriculturalists", primarily used slash and burn techniques for the clearing of the land (Williams 2008). Iversen found evidence of this in the form of charcoal in his pollen zone (Vera 2000). Important evidence for simultaneous agricultural activity and grazing of domesticated animals during time after the Neolithic Revolution over a large part of north-western Europe is given by a large number of pollen diagrams made over the past decades indicating burning of vegetation and the start of cereal cultivation (Rowley-Conwy 2004).

Interpretations

More recently however it has been pointed out that the history of the clearance of the closed forest that would have dominated Europe is far more complex than is explained by Iversens landnam theory. Before the Neolithic, in Mesolithic Britain, hunter-gatherers already used fire as a tool for forest clearing and subsequent cultivation of the land (Williams 2008). Vera (2000) also points out that later studies have sounded a note of doubt whether human activity alone can be contributed to the decrease of tree, and in particular elm pollen. Data is suggesting that a disease outbreak may have caused significant impact on the abundance of elm in north-western Europe. But despite these findings, the Landnam theory that Iversen and his followers describe are still used for the interpretation of palynological data (Vera 2000).

Many pollen records have been collected over the years. And even though the pollen data is often considered as fact, they are being interpreted differently when reconstructing the primeval landscapes (Bradshaw et al. 2003). In Vera's theory humans were not the cause of the sudden decline of tree species during the landnam period. In fact, since in his model closed forests did not have a dominating presence, large clearance of these forests did not occur either. A third interpretation of the facts could be that another climate change caused the sudden decrease of tree pollen. This theory however has been refuted for long time, since there is clear evidence of other increase of anthropogenic activity during the Neolithic Revolution (Godwin & Tallantire 1951).

Example studies

Vera's theory has been tested upon by several recent modelling studies and reviews combining many different sources. Svenning (2002) combined many studies and concluded that a correlation between the percentage of NAP and vegetation openness exists (see figure 3). It is also widely accepted that for the high amount of pollen of oak (*Quercus* sp.) and hazel (*Corylus* sp.), light-demanding trees, that are found in many pollen cores to be sustained a long period of time (e.g. more than 500 years) certain amount of openness should have existed (Bradshaw et al. 2003; Mitchell 2005). Some however point out that the open landscape Vera's describes could not have been the dominating landscape in primeval Europe often citing that there were not enough grazers to accomplish this (Mitchell 2005).

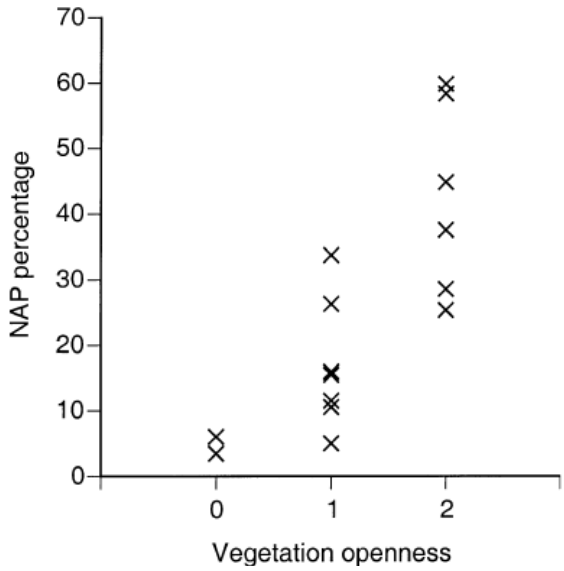

Figure 3 Svenning (2002) shows a convincing correlation between vegetation openness and non-arboreal pollen (NAP) percentages. These percentages were taken as the estimated averages of a number of pollen diagrams. Vegetation openness was scored as closed forest (0; n=2), mixed forest and open vegetation (1; n=8), and open vegetation with few trees (2; n=6). Source: Svenning (2002).

Mitchell (2005) looked at the relative amount of oak and hazel pollen from regions in Europe where it has been established that large herbivores had been present. He compared these with pollen data from Ireland, where historically due to geographic isolation large herbivores had been excluded until recently. One important point in Vera's theory is that large herbivores are essential for the rejuvenation process of oak and hazel, since these species are light-demanding and need more open landscapes to grow. Mitchell however found great similarities between the pollen records he compared which meant that oak and hazel did not have to be facilitated by the presence of large herbivores in Ireland.

Other studies show a more intermediate view in the debate (Bradshaw et al. 2003). Both closed forests and half-open landscapes can be present in local regions depending on the current conditions and the initial environmental parameters. On a longer time and larger space scale both types of landscapes could have been present with the same constant presence of grazing pressure (Kirby 2004). While this gives us the overall picture of the changing landscape of primeval north-western Europe, a call for more local-scale research was recently made. This because after recent local-scale study

on several pollen sites it was concluded that some sites conform to the closed forest theory and some to a more intermediate view (Fyfe 2007). Also ecological mechanisms at work in creating openness in vegetation structure, such as Vera's grazing by large herbivores, are often on a small scale.

II: Mechanisms

The appearance of earth's landscapes is not only formed by geomorphological processes but also largely by the ecological patterns of distribution and abundance of flora and fauna (Olff et al. 2009). When these landscapes are not transformed by anthropogenic impact, which was generally still the case before the Neolithic Revolution, natural occurring ecological mechanisms will play a large role in forming the vegetation structure. When talking about forest ecosystems, diverse disturbances such as floods, fires, wind-throw and grazing by herbivores are some of the factors, both abiotic and biotic, that influences the appearance and functioning of this system.

As mentioned earlier Vera's half-open landscapes only exist in certain circumstances. Here I will shortly explain the mechanisms of succession, ecological disturbances and associational resistance which are at work in the mosaic structure of Vera's half-open landscape.

Succession

After geomorphological processes such as landslides and erosion have acted upon an area, often a newly formed piece of bare ground forms. This area either already has or does not have a soil yet. When no soil existed, new substrate will eventually form. Either way the area will in time by colonized by plants flora and fauna often starting with lichens and mosses. In several stages, which can be of considerable different time lengths, the area will grow out unto a community of organisms. The classical succession theory states that this final stage is the climax. This is when the system becomes stable and stays stable when disturbances are an unusual event (Yamamoto 2000).

In the temperate region of north-western Europe forest ecosystems, will eventually be transformed from grassland, via scrubland, to closed canopy forests in which trees can regenerate in their own shade and in small gaps (Olff et al. 1999; Soepboer & Lotter 2009). This natural succession only occurs when the system is largely unaffected by regularly occurring disturbances such as herbivory, fire, flooding and diseases (Yamamoto 2000; Olff et al. 1999). Closed forest will then thus be the climax stage of succession.

This process of natural succession and has been shown to be an important concept in ecology for more than a century. The classical theory however was largely abandoned when it was discovered that disturbances do have a great impact on whether the climax stage of succession is stable since they can cause large gaps (Watt 1947).

Disturbances

Natural disturbances that influence the vegetation structure can be either classified as biotic or abiotic. The biotic factors that can influence forest ecosystems are grazers consisting of smaller and larger animals. While the abiotic factors that are most important in these systems are floods, fires and wind-throw. All these disturbances take part in the breakage of the closed canopy forest described as the climax stage of (classical) succession. The disturbances create gaps where new seedlings have a chance to grow due to the decrease of light competition. Watt (1947) famously describes these dynamics of forest ecosystems in his "Gap dynamics theory". This theory says that local sections of the forest go through several phases: gap, building and mature phases (Yamamoto 2000). And these disturbances are now considered to be the key factors in rejuvenating forests.

In Vera's theory Watt's gap dynamics have gone into the extreme. Closed forest can be completely broken down by disturbances (see figure 4). While the abiotic disturbances described act mainly on adult trees in the forest, the biotic factor of grazing retards recruitment. So when wind, fire and floods break down the high canopy, fresh seedlings will be consumed before they grow old enough. And even adult trees are being destroyed by the grazers since many species, such as red deer, are known to strip their bark (Soepboer & Lotter 2009). So Vera proposes that large herbivores were an important factor in giving the primeval landscape its shape since they kept this landscape from turning into a closed forest.

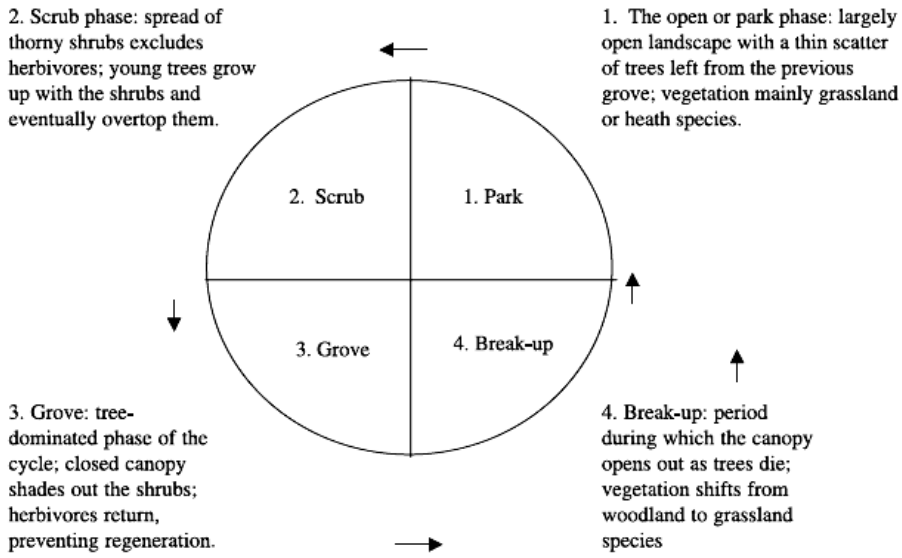

Figure 4 Vera's cyclical model according to Kirby, consisting of three phases: park, which is very open, scrub, which is half-open and grove, which is closed. Kirby added a fourth phase: the break-up. This represents the transition from closed grove back to open grassland (Park). Source: Kirby (2004)

But for the trees communities to still be able to rejuvenate in the system, another process should be at work. Otherwise closed forest breaks down to open grassland and does not turn into a park landscape (figure 4). Adaptations of tree species against disturbances exist in many forms. Abiotic disturbances mainly affect adults, thus adaptations against these factors are most apparent in the adult phase. Thick barks, strong stems and vertical growth form are some of these adaptations against the most common abiotic disturbances: flood, wind-throw and fire, with the last one playing a very important role during the late Holocene (post Neolithic Revolution) (Olsson & Lemdahl 2009). In Vera's view, herbivory by large grazers played an even larger role (Vera 2000). Strong adaptation against this biotic factor was therefore also needed for the park phase to continue into the scrub phase (figure 4).

Associational resistance

Associational resistance is a form of facilitation in which palatable species of plants are protected by other plant species from grazers. It is a common occurrence among plants and enables the seedlings from tree species to survive while being inside or close to an unpalatable species. In the temperate forest systems of north-western Europe this occurs when shrubs, such as blackthorn (*Prunus spinosa*) or hawthorn (*Crataegus* sp.) which are adapted to herbivory by thorns, spines, and chemical defences, protect palatable woody species such as oak and hazel (Vera 2000). Generally the more biomass of the unpalatable species there is in an area the more resistance. This only applies to large herbivores though, since small herbivores (such as rabbits) are not affected (figure 5).

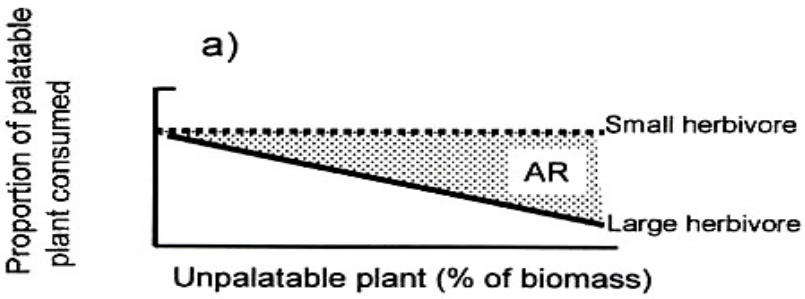

Figure 5 The advantage of associational resistance (AR) for the palatable is illustrated by comparing large herbivores which grazing is resisted against, with small herbivores which grazing is not resisted against. The more unpalatable plants in the vegetation patch the more resistance. (from (Olff et al. 1999)).

Thus it is this protection mechanism that is the explanation of how light-demanding woody species such as oak and hazel can rejuvenate in an area with presence of large grazers. This association between unpalatable and palatable species is seen as an adaptation against natural occurring herbivores that are now either extinct or are far less abundant in north-western Europe, creating an ecological anachronism (Bakker et al. 2004). Nowadays this particularly interaction between herbivores and woody plant species only occurs in wooded pastures such as New Forest, Borkener Paradies and Junner Koeland. Here the amount of free range large grazers is still sufficient to allow this process to occur and so this co-evolution continues here. Associational resistance is

therefore a key factor in Vera's theory which facilitated creating half-open landscapes across north-western Europe.

Shifting mosaics

As described earlier, in Vera's view the natural vegetation in the temperate region of north-western Europe consists of a mixture of large and small patches of grassland, regenerating scrubland and forested groves in which the indigenous fauna of large herbivores is essential for the regeneration of the characteristic trees and shrubs of Europe. Today's wood pastures can be seen as the closest modern analogy for this landscape (Vera 2000).

When combining the effects of natural succession which turns grassland into its climax vegetation of a closed canopy forest with the disturbance effects of herbivory and the mechanism of associational resistance, the dynamic landscape that will form has a quite different structure than Watt's gap-phase system. This structure is also referred to as a mosaic structure (Olff et al. 1999). An essential feature of Vera's model is that this mosaic structure is dynamic, changing over time in a cycle as pointed out in figure 4 and more illustrated in figure 6. The closed canopy forest should still partly exist as part of the cycle, however as groves which do not sustain themselves for a long period of time (Mitchell 2005).

In this closed forest phase the herbivores should still be part of the system and the population should not be dramatically decreased due to the relative low amount of herbs and seedlings of woody species to eat. Otherwise they cannot take part in the break-down phase needed to keep the cycle going (figure 4). The question then arises whether these grazers are controlling the structure of the vegetation or that the vegetation structure and availability of food controls the density of the grazers. If closed forest existed throughout the early- to mid Holocene, the grazer density must have been very low (Bradshaw et al. 2003). Grazers would have needed the gaps the were present in closed forests since this is where many herbaceous plant species favoured by the grazers are situated. At least in some parts of Europe it is shown that these grazers were not abundant enough to open up and enlarge the gaps (Bradshaw et al. 2003). This seems to imply that at least there, the structure controlled the density of grazers and not the other way around. The major

disturbance that influences the structure of the vegetation was then often fire, but this role has now been taken over by domesticated grazers who have greatly increased in numbers since the Neolithic Revolution.

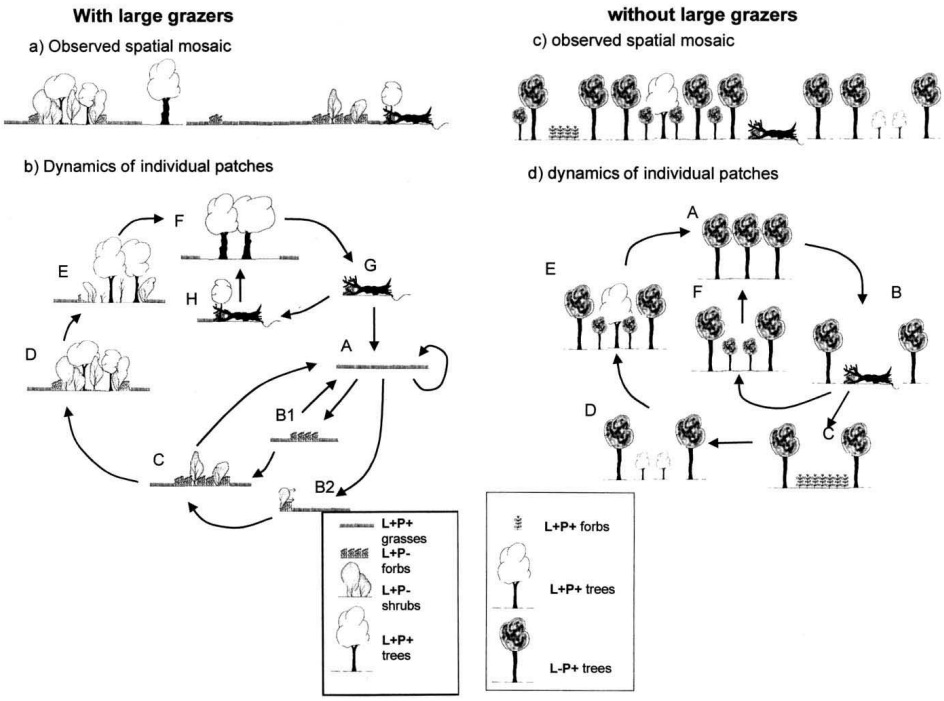

Figure 6 The structural difference of temperate forest systems with and without the presence of large grazers. Mechanisms like associational resistance give rise to a wood pasture type of landscape when grazers are present described by Vera. The absence of grazers leads to a more closed forest where Watt's gap dynamics (Watt 1947) cause rejuvenation. For details on the symbols and letters see source. Source: Olff et al. (1999)

III: Discussion & Conclusions

The Oostvaardersplassen, a 5000 ha nature reserve in the Netherlands, has been called today's live model of Vera's theory of a half-open landscape in which vegetation structure and composition is controlled by large herbivores. Vera played a large role in the long-term management decisions of this reserve (Vera 1988). In the reserve red deer, Heck cattle and Konik horses have taken the role of their past equivalents large grazers the elk, aurochs and tarpan. This combination of large grazers should in Vera's view have a positive effect on the system, since they are analogous to extinct species in similar systems in the past. Many conservation researchers look at the development of this reserve with much interest (Kirby 2004). Can the Oostvaardersplassen be a role-model for other reserves in Europe?

In the previously mentioned reserves New Forest, Borkener Paradies and Junner Koeland, the dynamic mosaic structure seems to actually be much more apparent than in the Oostvaardersplassen (personal observation). Differences in grazing intensity, but also in the amount of soil nutrients and productivity in the system make these systems very different. The famous Białowieża national park in Poland and Belarus is envisioned by Weisman (2007) to be last of the real wildernesses in Europe. Nowadays this system harbors many large grazers, including the wisent, but this system does not seem to be comparable to Vera's half-open landscapes. This only highlights the fact that not all forest ecosystems are the same and different systems need complete different conservation management approaches.

Shifting baseline

The primeval European landscape between the end of the last ice age and the Neolithic Revolution consisted mainly of environments with little human impact (Williams 2008). This Europe was surely very different than today's landscapes consisting of crop fields and pastures. In fact, at present no large lowland area of north-western Europe is completely without human impact (Peterken 1996). With its ever increasing human population it is hard to imagine a world without us (although some have tried to do just that (Weisman 2007)). The paleoecological studies I have described

can greatly benefit in understanding of how these past landscapes looked like and whether they can be recreated today. But the question remains what reference point in time to take when talking about recreating past landscapes. Between the last ice age and the Neolithic Revolution the landscape of north-western Europe was certainly not of a stable structure, since environmental conditions but also the amount of human impact changed during that time (Williams 2008).

According to Vera many people in our time have the wrong image when they imagine how the landscape looked like in primeval times. He ascribed this to the fact that today's goals of nature conservationists are not to recreate the natural environment before the major human impact, since these people grew up in an environment that consisted of cultivated land (Vera 2006). Since there is no present day reference point of land without human impact upon which nature conservationists can base their efforts in reconstructing forest ecosystems. Instead their benchmarks are the pre-industrial agricultural landscapes of the 19th century, where cattle, sheep and goats grazed on the land to keep the grass short. Using this strategy the biodiversity of plants on these places may be conserved, however the species that disappeared because of cultivation may never return (Vera 2000; Vera 2006).

So most nature conservationists agree that nowadays cultivation generally has a positive influence on biodiversity (Vera 2000). There are many species of herbaceous plants, and with them insects, that benefit from cultural activities that create open habitats (Bradshaw et al. 2003). On the other hand large scale land clearing has generally been shown to have a severe negative effect on biodiversity (Williams 2008) and the positive effect of historical cultivation practices may not outweigh this negative impact when comparing the overall biodiversity change. Present day conservationists face a difficult task in battling not only reduction of biodiversity, but also the loss of ecosystem functions (Olff et al. 1999).

Free range grazing

Since early farmers used slash and burn techniques and domesticated their cattle for grazing, humans have had their own disturbance impact on the landscape. However since the dawn of agriculture this impact has increased dramatically to a point that human

disturbances outweigh the natural disturbance mechanisms (Williams 2008). To assist in today's efforts in restoring nature and creating new nature reserves large herbivores are increasingly used in former agricultural areas (Olff et al. 1999). Free-range grazing regimes are used since it is believed that these will eventually create a more natural environment than ones where grazing is highly controlled by man.

It is however not necessarily automatically the case that free-range grazing regimes under today's environmental conditions will produce the same effect as herbivores did in primeval Europe. First off, the now extinct large grazers may have had functions in the ecosystem we do not know of, and unfortunately will probably never know (Olff et al. 1999). Furthermore no identical plant communities to the ones that occurred before the large human cultivation exist anywhere today, even under the same climatic conditions, and as a result today's plant-grazer interaction differs greatly from its primeval equivalent. Subsequently the assumption that is sometimes made that free grazing always benefits biodiversity more than controlled grazing is therefore incorrect (Kirby 2004).

To end the debate

Vera knows that a shifting baseline has occurred within the policy of nature conservation. However he also is afraid of the overuse of large grazers in this present policy in the Netherlands (Zeilmaker 2007). In the Oostvaardersplassen the positive influence of grazers on the system is apparent. There is however much discussion whether such a system can eventually be completely self-sustaining without human interference (Olff et al. 1999).

Although Vera's evidence for his theory has been called to question (Szabó 2009) and even rejected (Mitchell 2005) a number of times, the theory itself is still plausible to me. However the half-open landscape did not exist in the entire region of north-western Europe from early to mid-Holocene (Mitchell 2005; Bradshaw et al. 2003). But this does not warrant a total rejection of the theory, since conservationists can learn much from it (Moore 2005). The system of a half-open landscape has been modelled to be able to exist by many (Birks 2005; Soepboer & Lotter 2009). And at least in some regions the benefits

to biodiversity when creating a dynamic mosaic landscape with large heterogeneity has been shown (Olff et al. 1999).

Skeptics say that looking back into the past is largely irrelevant when discussing the present problems in conservation ecology since today's systems or not comparable to those of the past. Even the analogy of today's wood pastures with Vera's half-open landscapes of the past can be called to question since wood pastures are managed systems controlled by domestic animals even though they are free-ranging. But in my opinion looking back in the past using paleoecology and other tools can give us invaluable information. Co-evolution between species of plants and herbivores still exist today, although herbivores have been replaced by equivalents (Bakker et al. 2004). And even though today's systems can be different, studying the changes in past systems through time can help us predict what happens to systems today.

More recent paleoecological studies that are not only based on pollen research have been valuable in continuing the debate. Recent studies on dung-beetles for example also do not support Vera's theory. No dung-related beetle species fossils were found between 6300 and 1400 BC. Since the presence of dung beetles is thought to be directly related to the amount of large grazers, this (Olsson & Lemdahl 2009). Another example is the research on fungal spores whose presence can indicate a number of different human-induced impacts such as fire and the presence of non-free grazing animals which can ultimately tell us how much of an influence humans had on the vegetation structure (Blackford et al. 2006). These new developments show promise in resolving the debate since they can also help in enhancing the overall temporal resolution of reconstructions of past vegetation structure and improve our knowledge of the grazing intensity by large grazers in primeval Europe (Szabó 2009).

As of today the debate stimulated by Vera is still ongoing and many aspects concerning the openness of past forest ecosystems and disturbance mechanisms that form the structure of these systems are still not clear. Fully reconstructing past systems is not possible and not always desirable. But since Vera's theory and the debate has had and will have large implications I agree with many that further study should be conducted.

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