

Biodiversity in temperate European grasslands: origin and conservation

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Abstract

Northern Europe is in the forest zone, but wild megaherbivores have maintained grass-dominated vegetation here for the last 1.8 million years. Continuity of the grassland biome through glacial-interglacial cycles and connection to steppe vegetation has resulted in the evolution, immigration, and survival of a large number of grassland species. During the last millennia the effect of wild ungulates has been replaced by domestic grazers and hay making, and the persistence of grassland biodiversity depends on livestock farming. Local diversity is the outcome of colonisations and extinctions. Colonisations can be enhanced by maintaining networks of grasslands where species can migrate between sites, and by proper management that promotes establishment of new individuals. Extinction risk may be lowered in large grasslands, which may support large populations, and by proper management that promotes coexistence of species. Extinctions are accelerated by changes in environmental conditions favouring a few competitively superior plant species, especially increase in soil fertility. During the last century, natural grasslands in Europe have faced a dramatic loss of area and increased isolation of the remaining fragments, cessation of proper management, and increased load of nutrients. To achieve successful grassland biodiversity conservation there needs to be close cooperation between conservation managers and livestock farmers. For that, grassland management should take into account evolutionary and ecological rules behind the grassland biodiversity.

Keywords: biodiversity, conservation, evolution, species extinction, species richness

Introduction

Biodiversity conservation – preserving species and their genetic variability, ecological communities, and landscape variety is an urgent task for our society (Balmford *et al.*, 2005). Compared to other community types European grasslands have a rich flora and they may develop a very high small-scale species density (Pärtel *et al.*, 1996). For example, the highest vascular plant species numbers are found at the tiny scale of a few square centimetres to one square meter in temperate grasslands. In Laelatu wooded meadow in Estonia, 25 species of vascular plants have been described within 100 cm², and 42 species within 400 cm² (Kull and Zobel, 1991). In the same place 76 species of vascular plants have been described on 1 m² (Sammul *et al.*, 2003), which is the second highest record after 89 species in a shortgrass dry mountainous pasture in Central Argentina (Cantero *et al.*, 1999). High plant biodiversity is often reflected by high animal and fungal diversity, too (van der Heijden *et al.*, 1998; de Deyn *et al.*, 2003; Knops *et al.*, 1999). European grasslands are also rich in genetic variability within plant species (Prentice *et al.*, 1995; van Treuren *et al.*, 2005), contain many threatened species (Pärtel *et al.*, 2005) and they show a diverse landscape pattern (Jongman, 2002). Grasslands in the temperate zone usually persist due to moderate disturbance: grazing, mowing, or fires. During the last millennia temperate European grasslands have been mostly managed by grazing of domestic animals or by haymaking. This is the reason why

this ecosystem has often been 'semi-natural' (van Dijk, 1991). This fact does not imply that European temperate grassland as an ecosystem is man-made. It means that large grazing mammals are an integral part of this ecosystem, be it wild game or domestic livestock. In this respect, temperate European grasslands are not different from grasslands in other parts of the world with temperate climate. In warmer and drier climates, grasslands are conventionally thought to be climatogenic, i.e. constituting the climax vegetation under the prevailing climate conditions. Both mammal grazing and fire, however, are aspects of their ecology that have been somewhat overlooked in the past. Successional development of prairies, savannas, and steppes into woodland might take place if not halted by wildfires (Bond *et al.*, 2005) and grazing (Craine and McLauchlan, 2004) while alpine grasslands are characterized by low temperatures and grazing (Körner, 1999). Thus, most grasslands are dependent on various kinds of physical disturbance disfavoured by woody plants.

During the last hundred years drastic decline of grassland area and connectivity all across Europe has been detected (van Dijk, 1991). The main reason is that grassland farming is more efficient in cultivated stands than in natural permanent grasslands, but urbanization (Thompson and Jones, 1999) and air pollution (Stevens *et al.*, 2004) are also playing a role. Decline of European grasslands is threatening European biodiversity in all aspects, from genes to landscapes. For example in Finland at least 42 species of invertebrates, 4 species of vascular plants and 3 species of fungi which are primarily dependent on grasslands are already extinct and, respectively, 232, 60, and 38 species are threatened (Ikonen *et al.*, 2004). Combating this threat to biodiversity needs a new view of nature conservation (van Elsen, 2000). Traditional biodiversity conservation started with nature reserves from which all kinds of impacts by humans and their domestic livestock were excluded. In the case of European grasslands, strict exclusion of management by humans most often leads to a loss of grassland area due to succession into scrubland and forest. As most of the wild-living large herbivores are now extinct in Europe, grassland farming is important to biodiversity conservation (Sutherland, 2002). On the other hand, while abandoned grasslands that have undergone successional change into scrubland and forest can sometimes be reverted, grasslands that have been converted to arable fields undergo changes that are mostly irreversible.

There is still a long way to go to achieve successful cooperation between farming and biodiversity conservation (Kleijn and Sutherland, 2003). We are confident that the integration between effective grassland farming and biodiversity conservation is only possible if we follow the evolutionary and ecological rules of biodiversity dynamics in grasslands. There is, however, an optimistic outlook since agricultural research on grasslands is frequently concerned with biodiversity issues (Prins, 2004). In order to strengthen this contact we review (1) how the grassland biodiversity in temperate Europe has evolved, (2) what the main ecological rules are for maintaining high biodiversity, and (3) how this knowledge can be used for grassland biodiversity conservation and restoration.

Evolution of grassland biodiversity

The evolution and expansion of grasslands, with their uniquely coevolved grasses and grazers, took place during the Cenozoic (Retallack, 2001). The dominant plant group in grasslands, the grasses, originated at least 55 million years ago (Kellogg, 2001). Almost simultaneously, the first ungulates appeared (Janis, 1993). The shift of grasses to dominance in open habitats, i.e. the precursors of modern grasslands, however, took place much later. Likewise among ungulates, the grassland-dwelling bulk-grazer habit evolved later from an ancestral forest-dwelling browsing habit (Pérez-Barbería *et al.*, 2001; Janis *et al.*, 2002). True grasslands, and Serengeti-like communities of grazing animals, probably did not appear until the Late

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Miocene in the New World and the Pliocene in the Old World (ca. 5 million years ago).

At least throughout the Pleistocene (the last 1.8 million years), but probably much longer, grassland vegetation has existed in Europe. During this epoch, long cold and dry periods (glaciations) alternated with short periods of warm and moist conditions (interglacials) with an approximate 100 000 year periodicity (Zagwijn, 1992). During glaciations, steppe-tundra on permafrozen soils dominated in Central and Northern Europe, while xerothermic grasslands dominated in the Mediterranean basin (Van Andel and Tzedakis, 1996).

Temperate forest species probably survived in small pockets at micro-environmentally favourable locations in Central and Southern Europe (Bennett *et al.*, 1991), while boreal forest species may have had a distribution as open taiga-like vegetation intermingled with steppe-tundra (Willis and Van Andel, 2004). In terms of flora, the steppe-tundra was an intermediate between modern temperate grassland and tundra, or a mosaic of analogs of these biomes, generally having much drier and more alkaline soils than modern tundra (Yurtsev, 2001; Zazula *et al.*, 2003). In each interglacial, the development of ecosystems followed a recurrent pattern of balance between open and closed vegetation, i.e. between grassland/tundra and forest (Iversen, 1958; Bradshaw and Mitchell, 1999; Birks and Birks, 2004). In the first part of each interglacial, grasslands on alkaline or neutral un-leached soils dominated. They were gradually replaced by forests. At the end of previous interglacials, in which human interference has been negligible, grasslands on infertile soils gradually increased again (Iversen, 1964; 1969; Willis *et al.*, 1997; Wardle *et al.*, 2004).

Thus, grasslands have existed continuously in temperate Europe for millions of years, albeit with highly variable extent. This history of extension and contraction has shaped the biota of temperate European grasslands through speciation, extinction, and exchange of species with other biomes, such as steppes, temperate forest, alpine grasslands, tundra, and Mediterranean communities. A rich fauna of large mammalian herbivores was an integrated part of this grassland biome. During the penultimate interglacial, the Eemian (ca. 120 000 years ago), 17 species of large herbivores were native to lowland north western Europe (Svenning, 2002). Probably similar numbers have been present in all Quaternary interglacials except our own, the Holocene (Bradshaw *et al.*, 2003). Among these species were now (regionally) extinct elephant, rhinoceros, hippopotamus, giant deer, and buffalo, extant red deer, fallow deer, and bison, and species now found as domesticated livestock only, i.e. aurochs (cattle) and horse. During periods of maximum forest cover, grasslands and their associated biota survived in refugia, often in places where edaphic and climatic conditions have been suboptimal to trees (Ellenberg, 1988). Similarly to full glacial conditions, cold and dry places have prevented or retarded tree growth and regeneration and promoted grasslands. During interglacials, such conditions have mainly existed in alpine environments. In addition, warm and dry places, moderately unstable soils, and floods have promoted grassland resistance to woody plant invasion. These conditions have been found in a number of topographical and geomorphological situations, perhaps most prominently on shallow soils over solid rock or limestone preventing penetration of tree roots, and, in addition, steep slopes, sites exposed to strong winds, sandy infertile soils, and floodlands. To some extent, areas rich in such topographical features are at present-day relatively species-rich. Similarly, high-pH substrates tend to be more species-rich than low-pH substrates, due to the relative abundance of these substrate types in this biogeographical province during the evolution of the grassland floras (Pärtel, 2002).

Palaeoecological evidence of a grassland element in the landscape-scale vegetation comes from, among others, chalk hills in England (Bush and Flenley, 1987; Bush, 1993; Waller and Hamilton, 2000) and sandy infertile soils in Jutland, Denmark (Odgaard, 1994). One may

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hypothesize past synergistic effects of edaphic and topo-climatic conditions with disturbing agents such as fire and herbivores. Where wildfires created glades in the primeval forest, these would have been more resistant to forest regeneration under grazing by wild ungulates and under the described climatic and edaphic conditions.

Most plant species presently found in Central and Northern Europe are endemic to the temperate European grasslands and can only be protected here (Pärtel *et al.*, 2005). Traditionally, phytogeographers have been less interested in this general pattern than in exceptions to it. A number of plant species have characteristic distribution patterns, with main distribution ranges to the southeast or the southwest (Meusel, 1940; Meusel *et al.*, 1965). Plant species associated with contrasted edaphic conditions often exhibit widely differing distribution tendencies (Böcher, 1945). For example, plant species characteristic of grasslands on unstable infertile acid sandy soils are predominantly distributed in Western Europe, along the Atlantic coast. This pattern suggests that suitable habitat for these species has had a distribution more stable in time and space in this area than in Central and Eastern Europe. The genetic diversity of one species of this kind, *Carex arenaria*, increases southward to reach a maximum along the coast of the Bay of Biscay (Jonsson and Prentice, 2000), suggesting that this species survived the last full-glacial in refugia in this region or further to the south. Conversely, many plant species characteristic of grasslands on unstable infertile calcareous soils have distribution centres in Eastern Europe and scattered distributions in Central and Northern Europe. This pattern may indicate predominant survival of the last glaciation in steppe sites to the south-east, and subsequent (re)-immigration into Central and Northern Europe during late-glacial times and later (Pott, 1995). For the majority of species, which are endemic to the biome of temperate European grasslands, however, glacial survival in refugia far outside Central Europe is unlikely.

Pastoralism and arable farming, were introduced to Central Europe in simultaneous waves; ca. 5,000 BC (band-ceramic culture), ca. 1000 years later to Western Europe and ca. 2000–3000 years later to the Baltic area and Scandinavia (Champion, 1984). When selecting suitable areas for settlement, the first farmers probably sought out regions where, among other things, open pastures were easy to maintain, in other words, places where the edaphic and climatic conditions have been suboptimal to trees and natural grasslands were already present (Sammul *et al.*, 2000a). Arable fields created by slash-and-burn of forest, probably played a smaller role in rural economy, and took up considerably smaller areas, than pastures. As human populations grew, new areas were cleared of forest and turned into arable and pastureland (Pott, 1995; Bredenkamp *et al.*, 2002; Poschlod and Wallis de Vries, 2002). Plant and animal species from the natural grassland refugia in the primeval forest expanded appreciably in distribution, whereas distributions of forest organisms contracted. Some grassland species were probably redistributed, deliberately or not, considerable distances by humans and their livestock. In the Iron Age, hay meadows came into existence, providing a new and slightly different habitat for grassland biota. Despite some differences, in terms of qualitative impact on the vegetation, between hay making and ungulate grazing, the similarities are striking (Pykälä, 2000). Generally speaking, when agriculture was introduced, livestock grazing and haymaking replaced the grazing and browsing by wild megaherbivores. This is the solution to the apparent paradox that most conservation interests today are focused on apparently man-made habitats (Duffey *et al.*, 1974; Hillier *et al.*, 1990).

The agricultural practices of livestock grazing and haymaking, however, were not only beneficial to grassland biota. In many situations, arable farmers have exploited and exterminated grassland biota. For example, loess soils and deep rendzinas often support species-rich grassland communities, but are also profitable to arable farming. Thus, many

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grassland areas were turned into arable land or intensively managed rangelands (Bailey, 2000). The last wave of this development was seen in the Soviet agricultural expansion onto ‘virgin’ steppe lands, and similar expansions into vast natural grassland areas on other continents, but the exploitative position of arable farming with respect to grasslands has existed since the first farmers. Therefore, modern semi-natural grasslands, with their biota of native grassland species, are now found mainly in situations and locations unsuitable to agriculture, such as hilly terrain and shallow soils on rock outcrops and elsewhere.

Ecology of grassland biodiversity

Evolutionary processes have created a set of plant species that can sustain life in grasslands – the species pool (Zobel, 1992; Pärtel *et al.*, 1996; Zobel, 1997). Diversity at the smaller scale cannot exceed the limit set by the species pool, but, rarely reaches it (e.g. Collins *et al.*, 2002). Local diversity may be limited by lack of propagule dispersal, or by interactions in the local abiotic and biotic environment, e.g. competitive exclusion by superior species (Tilman, 1999), or lack of symbionts and presence of pathogens (de Deyn *et al.*, 2003).

The present climatic and land-use history has formed complex landscapes, where different vegetation types form a mosaic (Jongman, 2002). Grasslands have mostly occurred as fragments embedded in other types of vegetation. We can look at grasslands as ‘islands’ in the ‘sea’ of other type of vegetation: forests, wetlands, agricultural and urban areas. We shall use the term ‘patch’ for such grassland ‘islands’. Consequently, we can use the ‘equilibrium theory of island biogeography’ to explain how the level of biodiversity is determined by the balance between local immigration (dispersal and establishment) and local extinctions (MacArthur and Wilson, 1967). Nowadays, ‘metacommunity theory’ (set of dispersal-connected local communities) has partly taken over the island diversity theory (Leibold *et al.*, 2004).

In concordance with the theory, diversity is higher in grassland patches that are larger and better connected to other grassland patches, as shown in grassland fragments in Sweden and in Denmark (Köchy and Rydin, 1997; Bruun, 2000). Larger patches can support larger and genetically more diverse populations that have less dramatic population oscillations and a smaller probability to go extinct. Well-connected grasslands can get new species and genes which can build-up local diversity and replace these species and genes which have gone extinct. There are, however, other practical aspects too: larger and well-connected patches are probably more likely to be managed properly (grazing, hay-making). For grassland species, small fragments may not be large enough to support viable populations alone, but populations may still persist due to continuous inflow of propagules from surrounding populations. This phenomenon is called ‘spatial mass effect’ or ‘rescue effect’ (Shmida and Ellner, 1984; Kunin, 1998). Within a metacommunity small fragments are important components for the whole system and they may act as stepping-stones for dispersal.

Besides area and isolation, a grassland patch with different shape can have different potential for species gain and losses. Grassland margins are mostly less suitable for grassland species than the central areas (Luczaj and Sadowska, 1997; Morgan, 1998). This can be caused by shading from a neighbouring forest or by extra nutrient inflow (see below). Thus, grasslands round in shape have a higher potential for diversity due to higher area to perimeter ratio.

The surroundings of grassland patches are important for biodiversity, too. The ‘sea’ around a grassland patch may also support some grassland species (e.g. road verges, edges of ditches and fallow fields; Cousins and Eriksson, 2002), or they may be totally unsuitable for grassland species.

Species dispersal is a stochastic process. Ultimately dispersal is dependant on the distance to other patches (Coulson *et al.*, 2001) and on presence of dispersal vectors. Domestic animals

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can successfully act as seed dispersers (Fischer *et al.*, 1996; Kiviniemi and Eriksson, 1999; Couvreur *et al.*, 2004). In order to do this, however, they must be able to move from one site to another. Shepherding was once common in Europe, but has now almost disappeared (Poschlod *et al.*, 1998; Bruun and Fritzboeger, 2002; Suárez and Malo, 2002; Znamenskiy *et al.*, 2005).

Successful species dispersal requires considerable time. If grassland continuity has been interrupted, for example if the grassland has become overgrown by scrub or has been cultivated, to restore it again, seed dispersal will have to start from the beginning. Seed banks do not generally persist long-term in grassland soil (Kalamees and Zobel, 1998; Bakker and Berendse, 1999; Mitlacher *et al.*, 2002). If we consider the arrival of a new species as a random process, then, given more time, a site can 'collect' more species. Thus, age of a grassland patch is an important factor for generation of high diversity (Ejrnæs and Bruun, 1995; Kukk and Kull, 1997; Pärtel and Zobel, 1999). Even if a species is present in a community, dispersal can result in the establishment of new genotypes. For example, in an old calcareous alvar grassland on Öland, there was a large number of different genotypes of grass *Festuca ovina* found under different micro-environmental condition (Prentice *et al.*, 2000).

There are, however, plenty of examples which do not support the equilibrium island theory and suggest that present-day diversity is mainly determined by factors other than current area or degree of isolation (Simberloff and Gotelli, 1984; Eriksson *et al.*, 1995; Pärtel and Zobel, 1999). In recent studies this controversy has been solved. Due to recent rapid disappearance of grasslands the current patch size and isolation is completely different from that which occurred during previous centuries when the diversity was formed. Using historical maps we can look at former grassland areas and their isolation. These two characteristics describe actually the present-day diversity (Helm, 2002; Lindborg and Eriksson, 2004). This means that the present-day high diversity may be a remnant from a previous habitat area and connectivity and may not be supported by the current system. The time lag between increase of isolation over a critical level and subsequent loss of species may be 100 years or more, thus largely hindering our ability to make appropriate conservation decisions. If we do not ensure good species dispersal between sites in the future, extinctions are very likely to occur. This phenomenon has been coined the term 'extinction debt' (Hanski and Ovaskainen, 2002).

While landscape-scale processes determine the potential for plant community species richness (community species pool), local processes within the community determine the actual diversity at the site. When a new species has successfully arrived in a grassland patch, first it must be able to establish a new population. Secondly, it should be able to persist in competition with other species. Local diversity is always a balance between the input of propagules of different species, their establishment, and persistence in competition with neighbours (Mitchley and Grubb, 1986; Watt and Gibson, 1987). The local processes are mainly determined by grassland management, but moderate natural disturbances can also promote species' establishment and prevent competitive exclusion.

Grassland management affects the structure of the vegetation and determines the abundance and distribution of gaps in which propagules can establish. For example, it has been demonstrated that the litter layer which appears after abandonment of grazing or mowing strongly limits the germination of seeds and establishment of seedlings and leading to decline in diversity (Milton *et al.*, 1997; Foster and Gross, 1997; Tilman, 1997).

High small-scale diversity is only possible if many different individual shoots (ramets) can be 'packed' into a limited soil surface area. The conditions on grasslands are such that they not only enable close 'packing' of ramets but also enable close proximity of individuals

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of different species. The latter is only possible when competition between individuals is not strong enough to eliminate one of the neighbours. The common feature of all European species-rich natural grasslands is that they have a relatively low vegetation and low (but not the lowest) productivity. The mechanisms whereby intermediate levels of disturbance and/or intermediate levels of productivity coincide with the highest species density in grasslands (Grime, 1973; Connell, 1978; Huston, 1979) are still poorly understood (Palmer, 1994). Competition is considered asymmetrical when access to the resource that is competed for is monopolised. It is well known that competition becomes harsh and eliminative for subordinate species when it is asymmetrical (Weiner and Thomas, 1986; Peet and Christensen, 1988) and not interrupted by disturbance (Grime, 1973; Grime, 1977). In very broad terms, one can say that competition for above-ground resources (e.g. light or space) is often asymmetrical whereas competition for below-ground resources (water, nutrients etc.) is mostly symmetrical (Peet and Christensen, 1988). Nevertheless, there are multiple ways of how above- and below-ground competition interact in different species (Cahill, 2002), and the productivity of the community strongly influences the dynamics of competitive exclusion.

The availability of light to a single ramet depends largely on comparative difference in size of neighbouring ramets. When productivity of the site is high, plants obviously grow faster and difference between relative growth rates of neighbouring ramets leads to differences in size of shoots. Further on, the difference in size accumulates and species with low stature may become outcompeted unless they have some specific adaptations that enable them to tolerate low level of light availability or escape from competition. Enhanced productivity can reduce diversity when fertilisers are applied to natural vegetation (Smith *et al.*, 2000; Sammul *et al.*, 2003) and also during restoration of natural grassland in a habitat that previously received fertilizer applications and, thus, has high level of residual fertility (Marrs, 1993; Janssens *et al.*, 1998).

Continuous low-intensity management by mowing or grazing has a disproportionately large effect on competitive dominants, and by reducing the asymmetry in size distribution of plants it reduces the probability of competitive exclusion (Lepš, 1999). The reduced asymmetry of interactions is further amplified by the fact that uniform mowing and grazing balance the differences between different species in other aspects of population dynamics, such as mortality, reproduction, and vegetative propagation which are commonly ramet size dependent and constitute one part of competition for space (Barkham, 1980; Pitelka *et al.*, 1985; Weiner, 1988). Thus, beside the direct effect on development and species composition of the grassland (Austrheim and Eriksson, 2001; Cousins and Eriksson, 2001), management regime also influences the dynamics of species interactions.

Conservation and restoration of grassland biodiversity

The design of grassland conservation measures should acknowledge the different processes described above. We are proposing a simple five-point scheme that should be followed for decision-making at grassland biodiversity conservation.

- 1) Existing grassland habitats should be maintained for large scale stability. When conserving diversity of vegetation in natural grasslands, it is important to prevent large-scale destruction of habitat (e.g. ploughing, Smith *et al.*, 2000) and deterioration of habitat quality (e.g. fertilization). The establishment of diverse vegetation is an extremely long-term process, while all large disturbances destroy vegetation almost instantaneously. Moreover, even residual cultivation effects bias the flora to the favour of annuals and ruderal species (Donelan and Thompson, 1980; Graham and Hutchings, 1988). The most diverse and species-rich meadows having a prevalence of species with life-history

characteristics that show slow growth and low reproductive rates, i.e. characteristics of species of stable communities (e.g. Graham and Hutchings, 1988; Sammul *et al.*, 2003).

- 2) The genetic diversity should be kept since this is providing the material for evolution (Prentice *et al.*, 1995; van Treuren *et al.*, 2005). Genetic homogenisation is a threat when single seed sources are used in restoration. Grassland continuity and small-scale habitat heterogeneity also support high genetic diversity.
- 3) Species dispersal should be supported. This means that management should be planned at the landscape scale enabling spatial and temporal continuity of the grasslands. Thus, sound conservation management of grasslands should concentrate on enhancing immigration (i.e. improving connectivity between sites). This is particularly important in grassland systems that are facing with an extinction debt. So far, most conservation efforts have concentrated on preservation of valuable sites. While this is extremely important, one must consider, that in addition to valuable sites, also less valuable sites often need to be protected to create stepping stones, migration corridors and secure presence of metacommunity systems.
- 4) Recruitment of new individuals should be supported through preventing the formation of litter layer, promoting small-scale patchiness (e.g., scattered tiny gaps with mineral soil exposed), and allowing seed to ripen (e.g., late hay making).
- 5) Species coexistence should be supported. This means preventing competitive exclusion of small-size species by taller ones. This can be achieved by proper management which prevents large species (both large herbs or grasses and woody species) to dominate. On the other hand it is important to avoid activities that lead to increase in productivity of the site (e.g. fertilization, or supplementary feeding of livestock) as this would inevitably cause increase in the intensity of competition and thus also exclusion of subordinate species (Sammul *et al.*, 2000b).

Grassland destruction and fragmentation has in many regions already gone so far that long-term sustainability of biodiversity is questionable. Grassland restoration may reduce the extinction debt and alleviate the effect of fragmentation in the long-term. When considering restoring grasslands, it is important to set the goal of the action and qualitative criteria for evaluation of the success. Simply restoring the landscape is much cheaper than restoring the diversity of species and vegetation types.

The obvious limitation in restoration of grasslands is time. Natural species immigration is a long-term process. The estimated speed of natural species immigration in grasslands ranges several orders of magnitude (Gibson and Brown, 1991; Olff and Bakker, 1991). It has been suggested that restoration of grassland vegetation on arable fields could take up to 100 years if the seed supply is in close proximity (Gibson and Brown, 1992).

During the first phases of restoration it is important to focus on improvement of immigration.

In cases when connectivity between different sites is good, no addition of seeds or other propagules is necessary. During the first years grazing is better as the main management tool because animals transport propagules and thus increase the speed of formation of field layer. Later on grazing may be used in combination with or replaced by mowing.

When connectivity is not sufficient to support immigration, seed sowing may considerably increase the speed of development of grassland vegetation. While seed limitation obviously restricts the rate of colonisation (McDonald, 1993; Zobel *et al.*, 2000) and sowing of seeds speeds the dispersal process, it is important to keep in mind that the appropriate microsites for the species establishment are not always available (Jones and Hayes, 1999) and it might be difficult to find the appropriate mixture of species that would suit the particular microsite

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conditions. Moreover, sowing seeds actually creates a higher level of genetic and species composition homogeneity between neighbouring sites as two important factors that create differences between habitats – time of arrival of different species, and genetic differences between populations will be homogenised. Thus, in this way one would interfere with natural distribution of species (Akeroyd, 1994) and with microevolutionary processes (Ashley *et al.*, 2003). It is important to make a good compromise between speed of the restoration process and the natural state of the end product when making decisions about restoration. We suggest that the natural immigration process should be adhered to as often as possible.

While restoration of natural grasslands is a very powerful tool, it can never be used without first properly preserving the existing grasslands. Restoration efforts start to pay back in 20–50 years when species diversity of restored grassland starts to reach levels of persistent ones (Gibson and Brown, 1991; Olff and Bakker, 1991; Smith *et al.*, 2000). Without existing grasslands there would be no sources for natural species migration. Moreover, the preservation of grasslands is order of magnitude cheaper than restoration. For example, the analysis of management and restoration costs of Estonian meadows shows that restoration is 25 to 30 times more expensive in both dry boreo-nemoral and floodplain meadows whereas expenses of restoration increase by 50% with every 4 to 5 years after the abandonment in wooded meadows (Ehrlich, 2004). Although currently management of grasslands to maintain high biodiversity is often incompatible with management for maximum economic profit (Hodgson *et al.*, 2005) different subsidy systems can be developed to allocate conservation funds in a way that produces the best ecological effect (Wu and Bogess, 1999; Johst *et al.*, 2002).

Conclusions

While forest should be the most abundant ‘natural vegetation’ in temperate Europe, a large part of the European plant and animal species is associated with open habitats. This fact stresses the importance of conserving the biota associated with grasslands, even when they occur in apparently man-made ecosystems. As grasslands have developed over many centuries with permanent extensive use for agricultural purposes, and since this practice has often led to valuable and diverse sites, the farmers are at the heart of grassland conservation. Only extensive agriculture can preserve these areas. Grassland farming practice aimed at conserving or restoring biodiversity is not as economically profitable as conventional grassland farming. Our society has, however, set measures to compensate for the income difference, literally paying for biodiversity. Even if the support does not totally cover the loss of income, keeping the natural grasslands is a good investment for the future when awareness of biodiversity value will definitely increase. Since there is never a surplus of money in environmental support schemes, the most efficient local management techniques should be used. For that, proper well-replicated networks of grassland biodiversity management experiments are urgently needed at the national and European levels. Using the scientific knowledge on evolution and ecology of grassland biodiversity, effective grassland farming and biodiversity conservation can be integrated.

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References

- Akeroyd J. (1994) Seeds of destruction? *Non-native wild-flower seed and British floral biodiversity*. London: Plantlife.
- Ashley M. V., Willson M. F., Pergams O. R. W., O'Dowd D. J., Gende S. M., and Brown J. S. (2003) Evolutionarily enlightened management. *Biological Conservation*, 111, 115–123.
- Austrheim G. and Eriksson O. (2001) Plant species diversity and grazing in the Scandinavian mountains – patterns and processes at different scales. *Ecography*, 24, 683–695.
- Bailey A.W. (2000) Future of temperate natural grasslands in the Northern Hemisphere. In: Jacobs, S. W. L. and Everett, J. (eds) *Grasses: systematics and evolution*. Melbourne: CSIRO Publishing. pp. 361–368.
- Bakker J. P. and Berendse F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution*, 14, 63–68.
- Balmford A., Bennun L., Brink B. T., Cooper D., Côte I. M., Crane P., Dobson A., Dudley N., Dutton I., Green R. E., Gregory R. D., Harrison J., Kennedy E. T., Kremen C., Leader-Williams N., Lovejoy T. E., Mace G., May R., Mayaux P., Morling P., Phillips J., Redford K., Ricketts T.H., Rodriguez J.P., Sanjayan M., Schei P.J., van Jaarsveld A.S., and Walther B.A. (2005) The Convention on Biological Diversity's 2010 Target. *Science*, 307, 212–213.
- Barkham J. P. (1980) Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). I. Clonal growth seed reproduction, mortality and the effects of density. *Journal of Ecology*, 68, 607–633.
- Bennett K. D., Tzedakis P.C., and Willis K.J. (1991) Quaternary refugia of north European trees. *Journal of Biogeography*, 18, 103–115.
- Birks H. J. B. and Birks H. H. (2004) The rise and fall of forests. *Science*, 305, 484–485.
- Böcher T. W. (1945) Beiträge zur Pflanzengeographie und Ökologie Dänischer Vegetation, II. Über die Waldsaum- und Graskrautgesellschaften trockener und halbtrockener Böde. *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, 4, 1–163.
- Bond W. J., Woodward F. I., and Midgley G. F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologists*, 165, 525–538.
- Bradshaw R. and Mitchell F. J. G. (1999) The palaeoecological approach to reconstructing former grazing-vegetation interactions. *Forest Ecology and Management*, 120, 3–12.
- Bradshaw R. H. W., Hannon G. E., and Lister A. M. (2003) A long-term perspective on ungulate-vegetation interactions. *Forest Ecology and Management*, 181, 267–280.
- Bredenkamp G. J., Spada F., and Kazmierczak E. (2002) On the origin of northern and southern hemisphere grasslands. *Plant Ecology*, 163, 209–229.
- Bruun H. H. (2000) Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography*, 23, 641–650.
- Bruun H. H. and Fritzboøger B. (2002) The Past Impact of Livestock Husbandry on Dispersal of Plant Seeds in the Landscape of Denmark. *Ambio*, 31, 425–431.
- Bush M. B. (1993) An 11 400 year paleoecological history of a British chalk grassland. *Journal of Vegetation Science*, 4, 47–66.
- Bush M. B. and Flenley J. R. (1987) The age of the British chalk grassland. *Nature*, 329, 434–436.
- Cahill J. F. (2002) Interactions between root and shoot competition among species. *Oikos*, 99, 101–112.
- Cantero J. J., Pärtel M., and Zobel M. (1999) Is species richness dependent on the neighbouring stands? An analysis of the community patterns in mountain grasslands of central Argentina. *Oikos*, 87, 346–354.
- Champion T. C. (1984) *Prehistoric Europe*. London: Academic Press.
- Collins S. L., Glenn S. M., and Briggs J. M. (2002) Effect of local and regional processes on plant species richness in tallgrass prairie. *Oikos*, 99, 571–579.
- Connell J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302–1310.
- Coulson S. J., Bullock J. M., Stevenson M. J., and Owyell R. F. (2001) Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *Journal of Applied Ecology*, 38, 204–216.
- Cousins S. A. O. and Eriksson O. (2001) Plant species occurrences in a rural hemiboreal landscape: effects of remnant habitats, site history, topography and soil. *Ecography*, 24, 461–469.
- Cousins S. A. O. and Eriksson O. (2002) The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. *Landscape Ecology*, 17, 517–529.
- Couvreur M., Christiaen B., Verheyen K., and Hermy M. (2004) Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. *Applied Vegetation Science*, 7, 229–236.
- Craine J. M. and McLauchlan K. K. (2004) The influence of biotic drivers on North American palaeorecords: alternatives to climate. *Holocene*, 14, 787–791.
- de Deyn G. B., Raaijmakers C. E., Zoomer H. R., Berg M. P., de Ruiter P. C., Verhoef H. A., Bezemer T. M., and Van der Putten W. H. (2003) Soil invertebrate fauna enhances grassland succession and diversity. *Nature*, 422, 711–713.

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- Donelan M. and Thompson K. (1980) Distribution of buried seeds along a successional series. *Biological Conservation*, 17, 297–311.
- Duffey E., Morris M. G., Sheil J., Ward L. K., Wells D. A., and Wells T. C. E. (1974) *Grassland Ecology and Wildlife Management*. London: Chapman & Hall.
- Ehrlich Ü. (2004) Pärändkoosluste majandusanalüüs [Economic analysis of semi-natural communities]. In: Kukk, T. (ed) *Pärändkooslused [Seminatural communities]*. Tartu: Pärändkoosluste Kaitse Ühing. pp. 78–85.
- Ejrnæs R. and Bruun H. H. (1995) Prediction of grassland quality for environmental management. *Journal of Environmental Management*, 43, 171–183.
- Ellenberg H. (1988) *Vegetation ecology of Central Europe*. Cambridge: Cambridge University Press.
- Eriksson Å., Eriksson O., and Berglund H. (1995) Species abundance patterns of plants in Swedish semi-natural pastures. *Ecography*, 18, 310–317.
- Fischer S. F., Poschlod P., and Beinlich B. (1996) Experimental studies on the dispersal of plant and animals on sheep in calcareous grasslands. *Journal of Applied Ecology*, 33, 1206–1222.
- Foster B. L. and Gross K. L. (1997) Partitioning the effects of plant biomass and litter on *Andropogon gerardi* in old-field vegetation. *Ecology*, 78, 2091–2104.
- Gibson C. W. D. and Brown V. K. (1991) The effects of grazing on local colonisation and extinction during early succession. *Journal of Vegetation Science*, 2, 291–300.
- Gibson C. W. D. and Brown V. K. (1992) Grazing and vegetation change: deflected or modified succession? *Journal of Applied Ecology*, 29, 120–131.
- Graham D. J. and Hutchings M. J. (1988) A field investigation of germination from the seed bank of a chalk grassland ley on former arable land. *Journal of Applied Ecology*, 25, 253–263.
- Grime J. P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.
- Grime J. P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, 111, 1169–1194.
- Hanski I. and Ovaskainen O. (2002) Extinction Debt at Extinction Threshold. *Conservation Biology*, 16, 666–673.
- Helm A. (2002) Saaremaa loopealsete võrgustik. In: Puura, I. and Teder, T. (eds) *Võrkude teooria*. Tartu: Eesti Looduseuurijate Selts. pp. 56–60.
- Hillier S. H., Walton D. W. H., and Wells D. A. (1990) *Calcareous Grasslands: Ecology and Management*. Bluntisham: Bluntisham Books.
- Hodgson J. G., Montserrat M., Tallwin J., Thompson K., Diaz S., Cabido M., Grime J. P., Wilson P. J., Band S. R., and Bogard A. (2005) How much will it cost to save grassland diversity? *Biological Conservation*, 122, 263–273.
- Huston M. (1979) A general hypothesis of species diversity. *American Naturalist*, 113, 81–101.
- Ikonen I., Ovesen C. H., Klein L., Alanen A., Tórhallsdóttir A. G., Naruševičius V., Østebrot A., Lind A. 2004. *Fögrur er hlíðin – Fair is the blooming meadow. TemaNord 2004:564*. Copenhagen: Nordic Council of Ministers.
- Iversen J. (1958) The bearing of glacial and interglacial epochs on the formation and extinction of plant taxa. In: Hedberg, O. (ed.): *Systematics of to-day*. Proceedings of a symposium held at the University of Uppsala in commemoration of the 250th anniversary of Carolus Linnaeus. *Acta Universitatis Upsaliensis/Uppsala Universitets Årsskrift*, 1958, 210–215.
- Iversen J. (1964) Retrogressive vegetational succession in the Post-glacial. *Journal of Ecology*, 52sup, 59–70.
- Iversen J. (1969) Retrogressive development of a forest ecosystem demonstrated by pollen diagrams from a fossil mor. *Oikos*, 12S, 35–49.
- Janis C. M. (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics*, 24, 467–500.
- Janis C. M., Damuth J., and Theodora J. M. (2002) The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 177, 183–198.
- Janssens F., Peeters A., Tallwin J. R. B., Bakker J. P., Bekker R. M., Fillat F., and Oomes M. J. M. (1998) Relationship between soil chemical factors and grasslands diversity. *Plant and Soil*, 202, 69–78.
- Johst K., Drechsler M., and Watzold F. (2002) An ecological-economic modelling procedure to design compensation payments for the efficient spatio-temporal allocation of species protection measures. *Ecological Economics*, 41, 37–49.
- Jones A. T. and Hayes M. J. (1999) Increasing floristic diversity in grassland: the effects of management regime and provenance on species introduction. *Biological Conservation*, 87, 381–390.
- Jongman R. H. G. (2002) Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape and Urban Planning*, 58, 211–221.
- Jonsson B. O. and Prentice H. C. (2000) Allozyme diversity and geographic variation in the widespread coastal sedge, *Carex arenaria*. *Diversity and Distribution*, 6, 65–80.
- Kalamees R. and Zobel M. (1998) Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, western Estonia. *Acta Oecologica*, 19, 175–180.
- Kellogg E. A. (2001) Evolutionary history of the grasses. *Plant Physiology*, 125, 1198–1205.

- Kiviniemi K. and Eriksson O. (1999) Dispersal, recruitment and site occupancy of grassland plants in fragmented habitats. *Oikos*, 86, 241–253.
- Kleijn D. and Sutherland W. J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, 40, 947–969.
- Knops J. M. H., Tilman D., Haddad N. M., Naeem S., Mitchell C. E., Haarstad J., Ritchie M. E., Howe K. M., Reich P. B., Siemann E., and Groth J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, 2, 286–293.
- Köchy M. and Rydin H. (1997) Biogeography of vascular plants on habitat islands, peninsulas and mainlands in an east-central Swedish agricultural landscape. *Nordic Journal of Botany*, 17, 215–223.
- Kukk T. and Kull K. (1997) Püisniidud. *Estonia Maritima*, 2, 1–249.
- Kull K. and Zobel M. (1991) High species richness in an Estonian wooded meadow. *Journal of Vegetation Science*, 2, 715–718.
- Kunin W. E. (1998) Biodiversity at the edge: A test of the importance of spatial “mass effects” in the Rothamsted Park Grass experiments. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 207–212.
- Leibold M. A., Holyoak M., Mouquet N., Amarasekare P., Chase J. M., Hoopes M. F., Holt R. D., Shurin J. B., Law R., Tilman D., Loreau M., and Gonzalez A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613.
- Lepš J. (1999) Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. *Journal of Vegetation Science*, 10, 219–230.
- Lindborg R. and Eriksson O. (2004) Historical landscape connectivity affects present plant species diversity. *Ecology*, 85, 1840–1845.
- Luczaj L. and Sadowska B. (1997) Edge effect in different groups of organisms: vascular plant, bryophyte and fungi species richness across a forest-grassland border. *Folia Geobotanica et Phytotaxonomica*, 32, 343–353.
- MacArthur R. H. and Wilson E. O. (1967) *The theory of island biogeography*. Princeton: Princeton Univ. Press.
- Marrs R. H. (1993) Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Advances in Ecological Research*, 24, 241–300.
- McDonald A. W. (1993) The role of seedbank and sown seeds in the restoration of an English flood-meadow. *Journal of Vegetation Science*, 4, 395–400.
- Meusel H. (1940) Die Grasheiden Mitteleuropas – Versuch einer vergleichend-pflanzengeographischen Gliederung. *Botanisches Archiv*, 41, 357–519.
- Meusel H., Jäger E., and Weinert E. (1965) *Vergleichende Chorologie der zentraleuropäischen Flora*. Jena: Gustav Fischer Verlag.
- Milton S. J., Dean W. R., and Klotz S. (1997) Thicket formation in abandoned fruit orchards: processes and implications for the conservation of semi-dry grasslands in Central Germany. *Biological Conservation*, 6, 275–290.
- Mitchley J. and Grubb P. J. (1986) Control of relative abundance of perennials in chalk grassland in southern England. I. Constancy of rank order and results of pot- and field-experiments on the role of interference. *Journal of Ecology*, 74, 1139–1166.
- Mitlacher K., Poschod P., Rosén E., and Bakker J. P. (2002) Restoration of wooded meadows – a comparative analysis along a chronosequence on Öland (Sweden). *Applied Vegetation Science*, 5, 63–73.
- Morgan J. W. (1998) Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. *Journal of Vegetation Science*, 9, 181–190.
- Odgaard B. V. (1994) The Holocene vegetation history of northern West Jutland, Denmark. *Opera Botanica*, 123, 3–171.
- Olf H. and Bakker J. P. (1991) Long-term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *Journal of Applied Ecology*, 28, 1040–1052.
- Palmer M. W. (1994) Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica et Phytotaxonomica*, 29, 511–530.
- Pärtel M. (2002) Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, 83, 2361–2366.
- Pärtel M., Kalamees R., Reier Ü., Tuvii E.-L., Roosaluuste E., Vellak A., and Zobel M. (2005) Grouping and prioritization of vascular plant species for conservation: combining natural rarity and management need. *Biological Conservation*, 123, 271–278.
- Pärtel M. and Zobel M. (1999) Small-scale plant species richness in calcareous grasslands determined by the species pool, community age and shoot density. *Ecography*, 22, 153–159.
- Pärtel M., Zobel M., Zobel K., and van der Maarel E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, 75, 111–117.
- Peet R. K. and Christensen N. L. (1988) Changes in species diversity during secondary forest succession on the

Biodiversity in temperate European grasslands: origin and conservation

- North Carolina piedmont. In: During, H. J. (ed) *Diversity and pattern in plant communities*. The Hague: SPB Academic Publishing, pp. 233–245.
- Pérez-Barbería F. J., Gordon I. J., and Nores C. (2001) Evolutionary transitions among feeding styles and habitats in ungulates. *Evolutionary Ecology Research*, 3, 221–230.
- Pitelka L. F., Hansen S. B., and Ashmun J. W. (1985) Population biology of *Clintonia borealis*. I. Ramet and patch dynamics. *Journal of Ecology*, 73, 169–183.
- Poschold P., Kiefer S., Tränkle U., Fischer S., and Bonn S. (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science*, 1, 75–90.
- Poschold P. and Wallis de Vries M. F. (2002) The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. *Biological Conservation*, 104, 361–376.
- Pott R. (1995) The origin of grassland plant species and grassland communities in Central Europe. *Fitosociologia*, 29, 7–32.
- Prentice H. C., Lönn M., Lager H., Rosén E., and van der Maarel E. (2000) Changes in allozyme frequencies in *Festuca ovina* populations after a 9-year nutrient/water experiment. *Journal of Ecology*, 88, 331–347.
- Prentice H. C., Lönn M., Lefkovich L. P., and Runyeon H. (1995) Associations between allele frequencies in *Festuca ovina* and habitat variation in the alvar grasslands on the Baltic Island of Öland. *Journal of Ecology*, 83, 391–402.
- Prins W. H. (2004) A history of the European Grassland Federation, 1963–2003. *Grass and Forage Science*, 59, 2–7.
- Pykälä J. (2000) Mitigating human effects on European biodiversity through traditional animal husbandry. *Conservation Biology*, 14, 705–712.
- Retallack G. J. (2001) Cenozoic expansion of grasslands and climatic cooling. *Journal of Geology*, 109, 407–426.
- Sammul, M., Kull, K., Kuk, T. (2000a) Natural Grasslands in Estonia: Evolution, Environmental and Economic Roles. In: Viiralt, R. (ed) *Conventional and Ecological Grassland Management. Comparative Research and Development*. Proceedings of the International Symposium, Tartu July 4–6, 2000. Tartu: Estonian Agricultural University, Estonian Grassland Society, pp. 20–26.
- Sammul M., Kull K., Oksanen L., and Veromann P. (2000b) Competition intensity and its importance: results of field experiments with *Anthoxanthum odoratum*. *Oecologia*, 125, 18–25.
- Sammul M., Kull K., and Tamm A. (2003) Clonal growth in a species-rich grassland: results of a 20-year fertilization experiment. *Folia Geobotanica*, 38, 1–20.
- Shmida A. and Ellner S. (1984) Coexistence of plant species with similar niches. *Vegetatio*, 58, 29–55.
- Simberloff D. and Gotelli N. (1984) Effects of insularisation on plant species richness in the prairie-forest ecotone. *Biological Conservation*, 29, 27–46.
- Smith R. S., Shiel R. S., Millward D., and Corkhill P. (2000) The interactive effects of management on the productivity and plant community structure of an upland meadow: an 8-year field trial. *Journal of Applied Ecology*, 37, 1029–1043.
- Stevens C. J., Dise N. B., Mountford J. O., and Gowing D. J. (2004) Impact of Nitrogen Deposition on the Species Richness of Grasslands. *Science*, 303, 1876–1879.
- Suárez F. and Malo J. E. (2002) La dissémination endozoochore dans les pâturages méditerranéens et la transhumance. In: Fabre, P., Duclos, J. C., Molénat, G. (eds) *Transhumance - Actes des journées euro-méditerranéennes de la transhumance*. Saint-Martin de Crau, France: Maison de la Transhumance/Cheminements, pp. 247–262.
- Sutherland W. J. (2002) Conservation biology: Openness in management. *Nature*, 418, 834–835.
- Svenning J. C. (2002) A review of natural vegetation openness in north-western Europe. *Biological Conservation*, 104, 133–148.
- Thompson K. and Jones A. (1999) Human Population Density and Prediction of Local Plant Extinction in Britain. *Conservation Biology*, 13, 185–189.
- Tilman D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81–92.
- Tilman D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455–1474.
- Van Andel T. H. and Tzedakis P. C. (1996) Palaeolithic landscapes of Europe and environs, 150,000–25,000 years ago: an overview. *Quaternary Science Reviews*, 15, 481–500.
- van der Heijden M. G. A., Klironomos J. N., Ursic M., Moutoglis P., Streitwolf-Engel R., Boller T., Wiemken A., and Sanders I.R. (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396, 69–72.
- van Dijk G. (1991) The status of semi-natural grasslands in Europe. In: Goriup, P. D., Batten, L. A., Norton, J. A. (eds) *The conservation of lowland dry grassland birds in Europe*. Peterborough: Joint Nature Conservation Committee, pp. 15–36.
- van Elsen T. (2000) Species diversity as a task for organic agriculture in Europe. *Agriculture, Ecosystems & Environment*, 77, 101–109.

Pärtel et al.

- van Treuren R., Bas N., Goossens P. J., Jansen J., and van Soest L. J. M. (2005) Genetic diversity in perennial ryegrass and white clover among old Dutch grasslands as compared to cultivars and nature reserves. *Molecular Ecology*, 14, 39–52.
- Waller M. P. and Hamilton S. (2000) Vegetation history of the English chalklands: a mid-Holocene pollen sequence from the Caburn, East Sussex. *Journal of Quaternary Science*, 15, 253–272.
- Wardle D. A., Walker L. R., and Bardgett R. D. (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, 305, 509–513.
- Watt T. A. and Gibson C. W. D. (1987) The effects of sheep grazing on seedling establishment and survival in grassland. *Vegetatio*, 78, 91–98.
- Weiner J. (1988) The influence of competition on plant reproduction. In: Lovett Doust, J. and Lovett Doust, L. (eds) *Plant reproductive ecology*. Oxford: Oxford University Press. pp. 228–245.
- Weiner J. and Thomas S. C. (1986) Size variability and competition in plant monocultures. *Oikos*, 47, 211–222.
- Willis K. J., Braun M., Sümegi P., and Tóth A. (1997) Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology*, 78, 740–750.
- Willis K. J. and Van Andel T. H. (2004) Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quaternary Science Reviews*, 23, 2369–2387.
- Wu J. J. and Bogess W. G. (1999) The optimal allocation of conservation funds. *Journal of Environmental Economics and Management*, 38, 302–321.
- Yurtsev B. A. (2001) The Pleistocene “Tundra-Steppe” and the productivity paradox: the landscape approach. *Quaternary Science Reviews*, 20, 165–174.
- Zagwijn W. H. (1992) The beginning of the Ice-Age in Europe and its major subdivisions. *Quaternary Science Reviews*, 11, 583–591.
- Zazula G. D., Froese D. G., Schweger C. E., Mathewes R. W., Beaudoin A. B., Telka A. M., Harington C. R., and Westgate J. A. (2003) Ice-age steppe vegetation in east Beringia. *Nature*, 423, 603.
- Znamenskiy S., Helm A., and Pärtel M. (2005) Threatened alvar grasslands in NW Russia and their relationship to alvars in Estonia. *Biodiversity and Conservation*, ##, ###.
- Zobel M. (1992) Plant species coexistence: The role of historical, evolutionary and ecological factors. *Oikos*, 65, 314–320.
- Zobel M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, 12, 266–269.
- Zobel M., Otsus M., Liira J., Moora M., and Möls T. (2000) Is small-scale richness in a calcareous grassland limited by seed availability or microsite availability? *Ecology*, 81, 3274–3282.

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