

Review

Historical Landscape Perspectives on Grasslands in Sweden and the Baltic Region

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Abstract: A landscape perspective is generally recognized as essential for conservation biology. The main underlying reason is that species respond to features of the landscape at various spatial scales, for example habitat area, connectivity, and matrix habitats. However, there is also an “historical” component of a landscape perspective, which has not received similar attention. The underlying reasons for historical effects are that humans have influenced landscapes during several millennia and that species and communities may respond slowly to land use change. An historical perspective on landscapes also relates to how we perceive “natural” vs. “cultural” landscapes, and thus how conservation actions are motivated and valued. We review studies from Sweden and the Baltic region in the context of an historical landscape perspective, focusing on semi-natural grasslands, *i.e.*, grasslands formed by long-term human management for grazing and hay-making. Semi-natural grasslands are today a high concern for conservation. Historical effects are ubiquitous on species distributions and patterns of species richness, and have important implications for developing informed conservation programs in semi-natural grasslands, particularly with regard to assumptions of historical baselines, the choice of conservation targets, and insights on time-lags in the response of species to current landscape change.

Keywords: conservation baselines; extinction debt; historical ecology; remnant populations; semi-natural grasslands

1. Introduction

It is increasingly recognized that conservation biology should have a “landscape perspective” (e.g., [1–3]). This is generally understood spatially, referring to the importance of considering a target for conservation (a population, species, or a specific habitat) in a spatially extended context. This means for example that the landscape matrix surrounding a target object should be considered, and to account for potential source populations in the neighborhood for dispersal into the target area or to account for new, non-occupied, potentially important sites for colonization from the target area. A landscape perspective may also imply that the context of people living in or nearby the conservation target should be considered; their perceptions, values, and economic benefit, or loss, of conservation actions. Lindborg *et al.* [1] contrasted a landscape perspective with the undoubtedly more common “single object perspective” in conservation planning, concluding that in order to conserve successfully, and in the long-term, the focus should extend to whole landscapes.

Figure 1. Three semi-natural grasslands from Sweden. The top represents a grazed forest which is what many of the extensive forests that were grazed, up until 70-years ago, might have looked like. The grassland to the lower left represents a typical Swedish semi-natural grassland remnant, on very thin well-drained soils, that were not possible to turn into crop-fields. Note that Swedish grasslands have a fairly high abundance of trees and shrubs. According to 300-year old historical maps both grasslands have been managed for a very long time. The lower right photograph shows a shore meadow that is a result of grassland management but also land uplift, since 200 years ago none of the land in the picture would have been above sea level. However, as this shore meadow has been managed for many centuries there have been plenty of opportunities for plant colonization. Photos by Sara Cousins.



In this paper, we focus on a temporal dimension of the landscape perspective, *i.e.*, an historical landscape perspective. As we will show, such an historical landscape perspective implies more than just a narrative of “what has happened”? Landscape history in this context means that we explicitly consider a time-depth in the ecological processes that affect species, communities and landscape structure. This time-depth can be considered at different time-scales, thus associating with different ecological patterns and processes. We focus on “history” as it is understood in the humanities, *i.e.*, history of the human culture. This is not to deny that other historical processes may also be important to consider, for example long-term changes in species distributions resulting from climate change, or evolutionary processes acting over shorter or longer time periods. Our choice of a focus on history of human culture derives from the fact that the conservation targets we discuss—grasslands in Sweden and the Baltic region (Figure 1)—are products of the human culture, as they have developed during the last couple of millennia. Species-rich grasslands with a long history of management are targets for many conservation and restoration actions today.

There is a rich literature on the historical dimensions of landscapes; one may even say that the concept of landscape may not be possible to understand without references to history (e.g., [4–6]). Historical ecology [7] is inherently integrative, crossing over boundaries dividing what is usually considered as separate academic disciplines, most obviously ecology, archaeology, anthropology, geography and history. Balée [7] suggested a list of postulates defining historical ecology, based on the fact that a large fraction of environments on Earth have been affected by humans [8], and that this impact depends on socioeconomic and cultural context. Thus, research in historical ecology integrates both historical and ecological phenomena as they have changed over the course of time (e.g., [9]).

Recent reviews of historical ecology have stressed that knowledge of human history may provide important input for ecological studies (e.g., [10–12]). For example, Vellend *et al.* [12] illustrated how historical information may be used as ecological experiments, guiding predictions of the future (e.g., “to predict how species respond to climate change, let us see how they did respond previously, back in history”), but also as a means to assess delays in species response to environmental change. It is known that present-day patterns of species richness, particularly in grasslands, may reflect long-term management history (e.g., [13]), and that there may be time-lags in the response of species to land use change, contributing to an extinction debt [14,15]. The use of history to set up conservation and restoration goals can be considered as “applied historical ecology”. Furthermore, studies of historical human impact on landscapes have contributed to questioning the myth of a “pristine” wilderness without any impact from humans (e.g., [16,17]). Historical ecology is informative when it comes to questions of valuation in conservation biology. Many suggested values of landscapes are associated with history, such as “heritage”, “tradition” and “identity”, often considered as components of cultural ecosystem services [18]. Furthermore, the “old cultural landscape” in Europe, which is currently perceived as beautiful and thus valuable, was once a part of ordinary people’s livelihood [19]. The perception of this landscape today may be seen as part of a recent social construction, similar to the changing valuation and meaning (“re-interpretation”) that have occurred for other human products that have changed function, for example old abandoned industries in urban landscapes [20]. This relates to an important issue for conservation biology, namely how we define models for maintenance and restoration of landscapes shaped by human culture. For example, what is the rationale for choosing a certain time depth (age), based on historical maps or other sources, as such a model?

We present an historical landscape perspective of grasslands in Sweden, with some additional references to the whole Scandinavia and the Baltic region. We will first provide an overview of the historical context of these grasslands, serving as a starting point for a discussion of how an historical landscape perspective may influence the ways we value, manage, and restore, grassland habitats. Our main objectives are to show how an historical landscape perspective contributes to understanding: (i) why these habitats contain such high biodiversity; (ii) how patterns of biodiversity in grasslands respond to landscape change; (iii) why modern people value different aspects of historical landscapes, and finally; (iv) how an historical landscape perspective may guide choice of models for conservation in order to maintain as much of these grasslands as possible, for the future.

2. The Historical Context

Scandinavia and the region bordering the Baltic Sea (Figure 2) is located in Northern Europe, extending approximately from 55°N to 70°N, crossing the Polar Circle in the North. Despite this northerly position, the climate is quite benign due the influence of the Gulf Stream. The region encompasses several vegetation zones, from the nemoral zone in the south, through the boreal zone, and up to the arctic tundra in the north. A mountain range, the Scandes, stretches along the Scandinavian Peninsula, with altitudes up to over 4000 m.a.s.l., thus including large areas with alpine vegetation. This wide range of climatic conditions implies that the historical development of human cultural impact on the landscape varies considerably across the region. As the main topic of this review is an historical landscape perspective on grasslands, and how these developed in association with keeping of domestic livestock and agriculture (pastures, hay-meadows), we will focus on the southern parts of the region, where pasture and hay-meadow management was most common early in history.

Figure 2. Map of the region around the Baltic Sea in north-western Europe.



After the last glaciation, which had its maximum *ca.* 20,000 years ago, Scandinavia and the Baltic region were (re)colonized by vegetation, mainly from the south. Bands of human hunter-gatherers followed the retreating ice sheet and colonized Scandinavia from the south around 14,700 years ago [21]. Although these early hunter-gatherers may have had some influence on habitats and landscapes, the first major human impact is associated with the later expansion of agriculture, during the Neolithic. At the beginning of the agricultural expansion the landscape appeared to have been dominated by forests [22]. Grasslands in this region are generally a product of human management, resulting from deforestation (cutting, burning), creating land used for grazing or production of winter fodder for livestock [19]. The main exceptions are temporary successional stages after wildfires, and patchy stretches of grassland occurring along rivers, lakes and along the Baltic coast. Coastal areas of the Baltic Sea are subjected to isostatic land uplift after the last glaciation [23], which continuously produces new land, temporarily favoring grassland until forest trees colonize. These shorelines would have been natural grassland areas for grazing wildlife and later for domestic livestock and hay-making.

Agriculture spread across Europe in several waves [24], initially from the Middle East, reaching continental northern Europe *ca.* 5500 BCE (Before Common Era), Denmark and southernmost Sweden *ca.* 4000 BCE, and further north up to around 60°N in south-central Sweden by 1200–800 BCE [25,26]. The first major impact of agriculture was thus in Denmark and southern Sweden (e.g., [27]). Around 3200 BCE a trend is discernible toward increased openness of the landscape, associated with forest clearing [28]. Around 1000 BCE, *i.e.*, during the Bronze Age, forest cover was below 40% in these landscapes, and less than 10% close to presumed centers of human activity, as suggested by the presence of burial mounds [29].

A second major deforestation phase occurred during the transition from late Bronze Age (1000–500 BCE) to pre-Roman Iron Age (500 BCE–0 CE) [30–32]. Stabling of livestock is believed to have started during this period, probably associated with a deterioration of climate, but also possibly stimulated by the insight that manure increased crop yields, and thus stabling of livestock was an efficient way to collect the manure [32]. This promoted development of hay-making on managed meadows (also pollarding of trees) in order to produce winter fodder for the livestock. We can envisage a cultural landscape composed of mosaics of fields, meadows, pastures, and managed semi-open woodlands. In Sweden, the development during the late Roman Iron Age (*ca.* 100–400 CE) made up the geographic basis of provinces, probably initially as local chiefdoms, that later merged into larger units, ultimately developing to regions that today are part of present-day Sweden. These provinces formed developing administrative structures that existed during medieval times (from 1000 CE and onwards), and this regional structure is still largely recognized in Sweden [32].

Although slightly younger, also western Norway and Estonia were early centers of agricultural expansion. In western Norway a substantial forest clearing occurred around 1500 BCE (the Bronze Age), followed by expansion of heathlands [33]. In Estonia, there is evidence for pastoralism *ca.* 3200 BCE (the Neolithic), and later, 1800–500 BCE (the Bronze Age), an expansion of agriculture and primitive arable fields [34]. There is further evidence for a significant human impact on vegetation over the last four millennia in Estonia, for example favoring early-successional tree species (*Betula*, *Alnus*, *Salix*) and tree species associated with semi-open landscapes (*Quercus*) [35].

A considerable part of Scandinavia and the Baltic region is either a climatic border-zone outside the agricultural core areas (e.g., [36]), or extends over areas where agriculture is simply not an option

for people, due to climate. In Finland, onset of cultivation (slash-and-burn culture) around 600 CE has been found to have affected the landscape openness, even though permanent fields were not established until *ca.* 1000 CE [37–39]. In the forest regions in central Sweden, agriculture developed around 100–600 CE in the form of so called farm-shieling systems, with permanently occupied farms associated with summer farms used for dairy production and hay-making [40]. Even in the boreal forests of the north, a significant impact of human activity can be traced in the forest composition and structure, as evident from studies of the history of reindeer herding by the Sami people during the last four centuries [17,41]. Grazing by reindeer may have a considerable effect in alpine and subalpine areas, and although remote mountain areas are customarily considered as “wilderness”, it seems more accurate to consider also these areas as a cultural landscape, albeit much less intensively used by people [42].

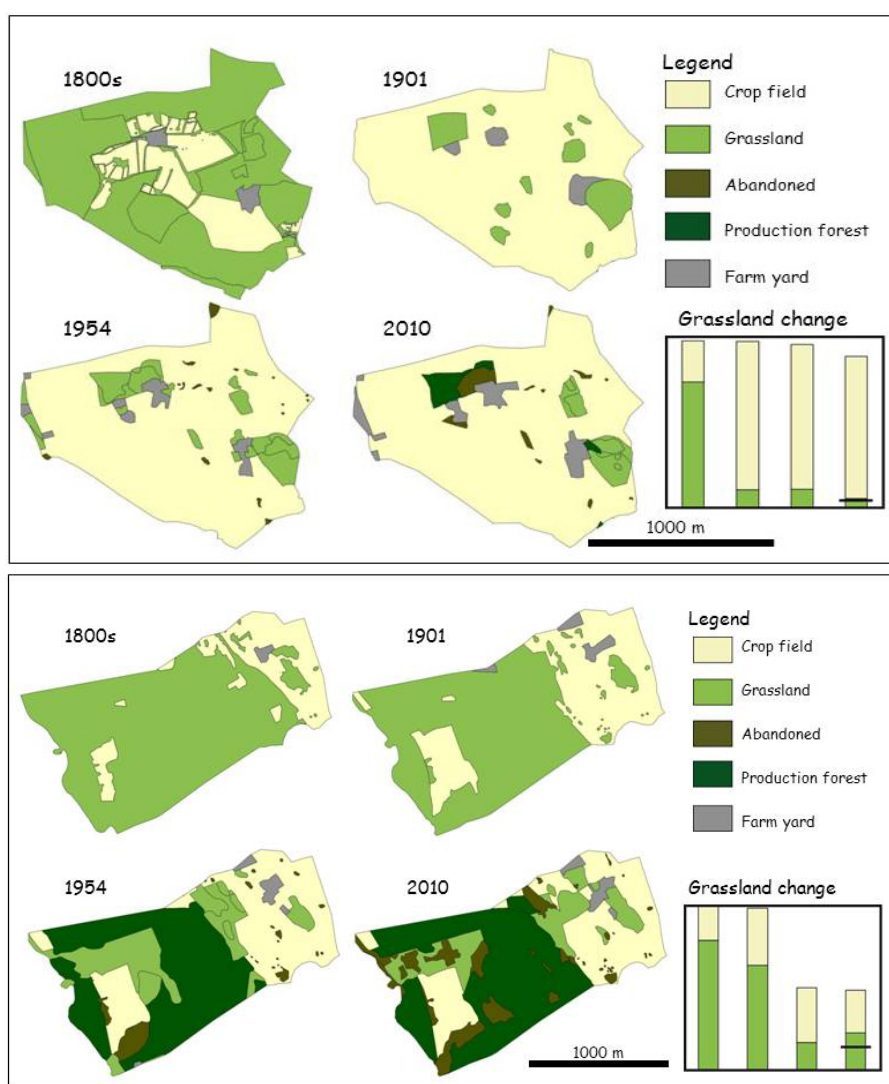
Returning to the core areas of agriculture, it seems as the direct human impact on structure and composition of vegetation and landscapes maintained an overall stability from medieval times, or perhaps even from the Iron Age [43], until the 18th century. This is not to deny that the cultural landscape was dynamic, with pulses of expansion and periods of decline and abandonment, particularly due to epidemics (like the Black Death in the 1350s) and climate variation [44]. But the overall means of resource use and the structure of villages, farms, fields, hay-meadows, and managed forests varied within rather narrow limits. Over large areas in southern Scandinavia the landscape structure was not much altered [28]. Indeed, in Denmark, the macro-scale pattern of three major land cover types, heathland, grasslands and patchy woodland has remained fairly stable for over *ca.* 3000 years [25,45].

During the period 1700–1870 the agricultural system changed drastically, motivating the often used term “the agricultural revolution” [46]. An account is here given for this change in Sweden [46], where the details of this transformation can be assessed based on the remarkable Swedish collection of cadastral maps from the 17th, 18th and 19th centuries (e.g., [47]). At the turn of the 17th century, the average population density in Sweden was four people per km², a quarter of the European average. The population was however unevenly distributed, with over twenty people per km² on the agricultural plains. Along with the general increase in science and technology promoted during the European Enlightenment in the 18th century, an increasing awareness of a potential food crisis stimulated modernization of agriculture, technologically as well as regarding land reforms. Redistribution of land (land enclosure; Swedish: “skifte”) was initiated, based on new legislation between 1750 and 1827. Increased forest clearing took place, as well as draining of lakes and wetlands to produce more arable land. New methods were introduced, crop rotation, use of artificial fertilizers, and production of winter fodder on arable fields (ley, usually clover-grass mixtures). All these changes implied a major transformation of the landscape, in turn strongly affecting grasslands, mainly due to using semi-natural grasslands for crop-production, and a declining use of grazing in forests. It is likely that this implied an increasing grazing pressure on remaining pastures supporting more animals per unit area. A second wave of modernization was initiated after the Second World War [48], drastically reducing the number of farms, and initiating a general abandonment of low productive arable fields and pastures, most of them becoming transformed to forest plantations as timber became one of Sweden’s most important commodities.

Several studies have estimated how these major landscape transformations have affected land cover, particularly grasslands. Cousins [49], using cadastral maps from 17th and 18th centuries, 1901 and aerial photos from 1950s and today, examined land cover changes in 12 study areas in south-central Sweden, south of Stockholm (Figure 3). Two hundred years ago 80% of the infield area was grassland for winter fodder. Livestock grazed the areas outside the village infield system, the infield areas after harvest, and every second year when crop fields were resting. Thus many small features, besides meadows, were managed as grasslands within the infield system, for example grass verges along ditches and roads, and bedrock and moraine outcrops (mid-field islets) in fields. Grasslands declined in two steps, between 200 and 100 years ago when grasslands on clay and silty soils were drained and turned into crop fields [49] and later, after the 1940s, grasslands on thin soils on bedrock or moraines were either planted with forest or abandoned. Forest grazing was banned 1928 with the intention to produce more timber in Sweden. Although livestock still grazed forests land until after the Second World War, farmers were ultimately obliged to plant “non-productive” land, *i.e.*, grassland, with forest in the 1950s. Legislation by the Swedish government 1948 implied that farmers and small-holders should have the same income as industrial workers, which meant that those that did not fulfill this criterion had to move from cottages and to sell small farms. These modernizations and political decisions caused the grasslands to further decline. As an example, on Selaön, a large island in the Swedish lake Mälaren, close to Stockholm, very small changes in land cover occurred between 1640 and 1854, but between 1854 and 1954, grasslands declined from an overall cover of 60% down to 5% [50,51]. A similar trend can be seen in other parts of the Baltic region, for example in Finland [52] and in Estonia [53].

The main themes of this overview of the historical context of grasslands in Scandinavia and the Baltic region can be summarized as follows: (i) grasslands are mainly a product of human culture, and since the Neolithic grasslands have functioned to feed livestock, as pastures, and from the Iron Age, as hay-meadows; (ii) thus, these grasslands can only be understood in the context of a long history of human management, grazing and hay-making; (iii) even though elements of very old landscapes still remain (for example grasslands associated with burial mounds), these landscapes have largely been transformed during the last few centuries; (iv) this implies that remnants of historical grasslands occur scattered in the modern landscape, often as small landscape fragments in a matrix of production crop-fields or forests. In the following, we will use the term *semi-natural grasslands* to denote grasslands with a long continuity of management, and which have not been sown, ploughed or fertilized, but have developed as an effect of deforestation combined with grazing or hay-making. Currently, there are about 500,000 ha of semi-natural grassland left in Sweden [54]. Although this may seem as a large area, it represents but a small fraction, probably less than 10%, of the area of semi-natural grasslands existing just a century ago. Today the majority of remaining Swedish semi-natural grasslands occur on thin well-drained soils that were not possible to cultivate. As we will show in the following, such remnant semi-natural grasslands are important for conservation, both for actions focusing on species and species diversity, and for actions focusing on other values, for example aesthetic and cultural.

Figure 3. More than 200 years of land use change from two infield systems in south-eastern Sweden [49]. **(Top)** The top landscape, Kallmyra, is situated on mainly clayey soils where grasslands were turned into crop fields more than 100 years ago. Today this is a typical open Swedish agricultural landscape. The landscape at the bottom, Ettersta, represents a landscape that changed later, mainly in favor of forestry, when grasslands were abandoned or planted with coniferous forest 70 years ago. **(Bottom)** The staple diagrams show the change in grassland (green) and crop field (yellow) during the four time-steps, with the oldest to the left. The line crossing the grassland staple in the present-day landscape represents the proportion of old semi-natural grassland within the landscape.



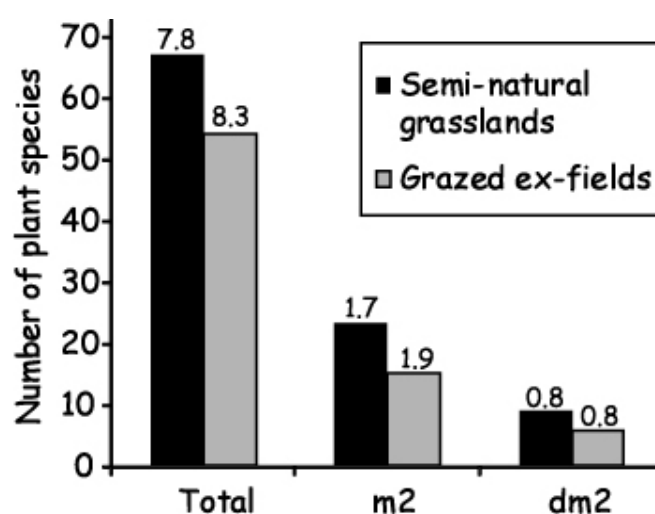
3. Biodiversity in Semi-Natural Grasslands

There is very strong evidence that the long-term impact of human agriculture has had a generally positive effect on local and regional biodiversity, and that this positive effect is manifested for a broad range of organism groups, for example plants, insects and birds (e.g., [55]). The biodiversity effects of semi-natural grasslands and other small biotopes in agricultural landscapes is obvious when considering the occurrence of red-listed species. Although this kind of data is not uncomplicated to interpret, for Sweden, the fraction of red-listed species associated with agricultural landscapes is generally high:

vascular plants (68%, $n = 402$), butterflies and moths (72%, $n = 504$), hymenopterans (81%, $n = 186$) and birds (49%, $n = 95$) [56]. From a biodiversity conservation viewpoint, these figures illustrate the importance in maintaining and restoring landscapes with semi-natural grasslands.

Local plant species richness is very high in still managed semi-natural grasslands with a long historic continuity, and clearly exceeds other recently created grasslands, for example pastures on ex-arable fields (Figure 4.). Grazing management is necessary to maintain plant species richness in semi-natural grasslands, but high species richness is also positively associated with a long continuity of grazing management in semi-natural grasslands [13,57–60], suggesting that the “time-depth” of these grasslands is essential for current diversity patterns. The significance of grazing management with a long historical continuity is not only evident for the core areas of agriculture, but also for maintaining diversity of plants in marginal areas such as sub-alpine and alpine grasslands [42,61] or on small islands in the archipelago [62].

Figure 4. Mean number of plant species found in semi-natural grasslands and grazed ex-arable fields (used as pasture no further back than the 1950s) in south-eastern Sweden. Grasslands in five different landscapes were investigated and total number of plants found in ten 1-m² plots within each grassland type per landscape, the mean number of plants per 1-m² plot (maximum was 39 species/m²), and five 10 × 10 cm plots within each 1-m² plot (500 samples) (maximum was 20 species/dm²). The figure above each bar denotes standard error. Data from [49].



Several mechanisms have been suggested to lie behind a positive relationship between local plant species richness and long continuous management by grazing or hay-making in semi-natural grasslands. The continuous removal of biomass hinders the process of competitive exclusion, thus allowing for coexistence of many species, even forbs of low stature and short life-span, which otherwise may have difficulties to maintain populations in a grassland matrix. Three factors promoted colonization rates of species in semi-natural grasslands, increased grassland area, stabilized location of grasslands due to permanent settlements [63], and increased dispersal [64–66]. Viewed in a meta-population context, increased colonization rate and reduced local extinction rate is expected to lead to an accumulation of species at local patches [63,67,68]. Indeed, it is often the case that about a third of the plant species

which are found at grassland sites covering several hectares, are found even in single plots sized 0.25 m² [69], *i.e.*, “species are everywhere”. This species accumulation process, operating over long periods of time, for several centuries or even millennia, ultimately produced very high local species densities, such as those typical for semi-natural grasslands [70]. An additional mechanism that have been suggested is that the increasing availability of grassland habitat resulting from human agriculture promoted niche shifts of species occurring in the pre-agricultural landscape, toward habitat niches characterized by increased openness and small-scale disturbance caused by grazing or hay-making [63].

Although it is very difficult to assess trajectories of change in local and regional species richness over time spans of several millennia, available evidence, based on pollen records, suggests that plant species richness was positively associated with periods of expansion of agriculture, from mid-Holocene up to modern times [71,72]. In a study from Estonia, Pärtel *et al.* [73] found that present-day plant species richness, both at a regional and at a local scale, was positively correlated to estimated human population density during late Iron Age (around 1000 CE), indicating that the most intensively used landscapes, although not what we would call intensive today, also were the most species-rich.

Furthermore, the human transformation of the landscape over the time from the Neolithic and until quite recently created a mosaic landscape. Although the landscape on the most productive agricultural plains was mostly open (e.g., [45]), there was room for a mosaic of several land cover types, for example including patches of semi-open woodland, and numerous small biotopes such as clumps of or single large trees (e.g., oaks), water ponds, ditches and stone walls. The managed semi-natural grasslands were more diverse as habitats compared with today, as they occurred on many different types of soils with various degrees of wetness and fertility. Today, most grassland are on thin, well-drained soils with low productivity. A varied and heterogeneous landscape including semi-natural grasslands, favors many animal species, for example butterflies [74] and birds [75].

However, it should be remarked that the clearing of forests commencing in the Neolithic and continuing up to the 18th century may have had some negative effects as well. However, except from single species of large mammals, for example the auroch [76], we find no evidence suggesting that species have gone extinct due to human impact from the initiation of agriculture, at least not until the last modernization of agriculture and forestry during the 20th century. The past diversity of habitats and the landscape heterogeneity is likely to have buffered any direct negative effect on species that may have resulted from clearing of forests.

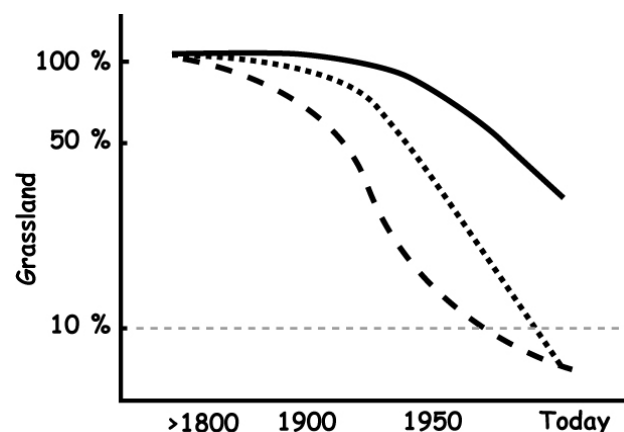
4. Effects of Delayed Species Response

The previous sections show that one of the most important insights from an historical landscape perspective on semi-natural grasslands is that current patterns of species diversity is a reflection of past landscape management that, at least on a landscape scale, no longer exists [12,13]. For plants in particular, local populations may be persistent long after the population growth has become negative, a phenomenon termed “remnant populations” [77]. Remnant populations can be seen as a temporal analogue to source-sink populations, where the present-day “sink” is supported from a “source” which existed some time ago. Among species inhabiting semi-natural grasslands, features such as clonality, possession of a perennial bud bank, and lack of features promoting long-distance seed dispersal have been found associated with the tendency to develop remnant populations [78]. Occurrence of a

persistent seed-bank is also likely to promote development of remnant populations [77,79], although seed-banks are depleted over time [80]. Thus, a prediction is that patterns of species composition and richness in remaining semi-natural grasslands should more reflect previous historical landscapes than current landscapes, for example in relation to habitat size and connectivity. This prediction was confirmed by studies in Sweden [14,58] and Estonia [15]. The time scale of this delay in plant species response was found to be in the magnitude of a century [14,81,82]. These results are important for conservation biology. If conservation planning is overlooking that present-day patterns of high biodiversity reflect an historical landscape, and not the present-day landscape, there is a risk of misinterpretation of the importance of size, connectivity and management of target habitats for conservation. Furthermore, remnant populations are declining, albeit slowly. Thus, even species that are still rather common may be at a risk of extinction in the coming decades. On the other hand, the occurrence of remnant populations implies that there are good opportunities for successful restoration of grasslands, for example at sites where management has ceased but biodiversity still remains.

The fact that many grassland species persist in a state of slow decline, and that patterns of species composition and richness reflect historical but not present-day landscapes, suggest that there is an extinction debt [83], *i.e.*, a fraction of the species-pool will go extinct in the near future under current landscape conditions. For plants in semi-natural grasslands, the existence of an extinction debt is related to the remaining fraction of semi-natural grassland left in the landscape [81]. For landscapes with less than 10% remaining semi-natural grasslands, no evidence of an extinction debt was detected, suggesting that the extinction process already been settled for the pool of grassland plant species that are not thriving in the modern landscape (Figure 5). Several studies in strongly transformed landscapes have reached a similar conclusion, *i.e.*, a very weak or non-existent “historical signal” on patterns of present-day species composition and diversity [51,69,84]. This implies that restoration of grasslands may not count on existing remnant populations as a source for re-creating past levels of diversity.

Figure 5. Illustration of trajectories representing grassland decline, in relation to a threshold (10% of remaining grassland area), below which extinction debt has not been detected. Thus, below this threshold the extinction debt is “paid”. The two broken lines represent different trajectories for strongly transformed landscapes, and the solid line represents landscapes with a considerable amount of semi-natural grasslands left. The figure is a generalization of data presented in [81].



We may then ask to what extent plant species in the current, transformed, landscape are able to disperse among sites where suitable grassland habitat occurs. There is much evidence that the answer to this question is that plants will not, within a reasonable time frame, manage to colonize isolated grasslands. Plants in semi-natural grasslands are generally dispersal limited [68,85,86]. Features promoting long-distance seed dispersal were most likely important in the processes that historically led to the formation of the species-rich grasslands (as mentioned above), whereas at present the most important features for still remaining plant species are related to persistence [87]. The temporal scale for reassembling semi-natural grasslands, even when potential source populations are situated nearby, is in the magnitude of 50–100 years [88]. Accordingly, even if many grassland plant species are left in the seed bank for some time [79,80], we may expect a “colonization credit”, *i.e.*, a delayed response in the colonization process at the local scale. This insight is relevant for restoration programs of semi-natural grasslands. Even if there are remnant habitats left in the landscape, for example midfield islets, that promote colonization of restored semi-natural grasslands [89], plant species that have gone extinct before the restoration commences are not likely to recolonize within relatively long periods of time [88,90–92].

From this overview of delayed species responses, we conclude that an historical landscape perspective is in several ways important for understanding patterns of species occurrence and diversity in semi-natural grasslands. It contributes to understanding why these habitats became so species-rich in the first place. The often slow response of species to ongoing landscape change implies that we need knowledge of previous historical landscapes in order to fully understand the current situation. Overlooking this historical aspect may lead to erroneous interpretations of the current status of species and communities, and thus to misguided conservation actions. Although this research field is still in its infancy, we need an historical perspective to put figures on the time scales for various kinds of change in populations. For the phases of species decline we may ask: Is there an extinction debt? How long does it take before it is paid? For the phases of increasing diversity, for example after restoration, we may ask: Are there remnant populations available that may regain a positive growth rate? How long does it take before species are able to (re)colonize? For answering any of these questions, an historical landscape perspective is necessary.

5. Perception and Valuation of Semi-Natural Grasslands

The preceding sections have focused on the biodiversity values of semi-natural grasslands, stressing that an historical landscape perspective is necessary both to understand the mechanisms behind diversity patterns and how species respond to ongoing landscape change. An historical perspective is however useful also when considering how society and people value semi-natural grasslands, and other remaining elements of the old-fashioned landscape. Antrop [5] described how conservation of nature and culture became fashionable in the late 19th century, along with historical “romanticism”, often with a nationalistic flavor, and that after an interregnum of neglect this interest in cultural landscapes in Europe has increased again during the last decades. This general interest, together with the high biodiversity values of semi-natural grasslands and other habitats associated with the cultural landscapes provides the basis for several conservation initiatives in the European Union [93] and Sweden [94].

As conservation goals and actions related to “old-fashioned landscapes” with semi-natural grasslands may be costly, and may affect many different aspects of society, an important issue is to understand the rationale behind people’s valuation of landscapes where semi-natural grasslands remains being a significant element.

In a thought-provoking paper, Orians and Heerwagen [95] summarized evidence and argued for the idea that humans have a biologically innate tendency to appreciate certain landscape features. The basis for this idea is that the long period of time during which humans were hunter-gatherers would have provided the ground for selection on habitat and landscape preferences promoting fitness. The operating proximate mechanism for this innate tendency for appreciation of certain landscapes would be emotional, manifested for example as aesthetical preferences. The preferred landscapes would, according to Orians and Heerwagen, be savanna-like, providing overview, shelter and food resources, and include elements such as water, large trees, a focal point, changes in elevation, semi-open space, distant view of horizon, moderate degree of complexity, and, as further suggested by Kaplan [96], an element of “mystery”, for example a bend around a hill or meandering streams, indicating that something could be discovered after further exploration of the environment. Orians and Heerwagen [95] did not deny the influence of cultural experiences on preferences for other types of landscapes, but suggested that people have a generalized bias towards such savanna-like landscapes, although life-long experiences may create attachment to other landscape features. Several authors have suggested that humans have evolved into a “cognitive niche”, or a “cultural niche”, encapsulating flexible cognitive abilities such as learning, communication and knowledge transfer, which form the basis for the exceptional capacity of humans to both construct, and adapt to, environments of different kind [97–99]. The agricultural landscape is perhaps the best example of such a constructed environment. It may thus not seem altogether farfetched to presume that this landscape construction has been influenced by an innate tendency—if such a tendency indeed exists—for preferences of certain landscape elements.

In Europe there has been extensive research on people’s attitudes to nature and nature conservation, relating to the issue of what kind of landscape elements and features people appreciate and value (e.g., [100–103]). Most of these studies, however, are based on a completely different paradigm than the one outlined by Orians and Heerwagen [95]. The dominating framework for most socially oriented landscape studies is instead social constructivism, *i.e.*, the idea that the “landscape” is merely a social construct (e.g., [6,104–106]), for example manifested as constructed images of nature: “arcadian”, “functional” or “hedonistic” [101,107]. Based on studies conducted in the Netherlands, Buijs *et al.* [107] further suggested that people’s valuation of landscapes in Europe has changed from a dominance of functional aspects to become increasingly influenced by a view where landscapes are seen as leisure commodities. However, other studies provide a different picture. For example, in interview studies conducted in Sweden, it was found that valuation of landscapes, and thereby motivation for conservation, included preservation of open land, serenity and cultural heritage, *i.e.*, history [100,108]. An interesting difference between countries and continents was reported by Saltzman *et al.* [109]. When they compared attitudes to agricultural landscapes in Sweden and Australia, they found that people in Sweden perceived agriculture as belonging to “nature”, whereas in Australia, which has a very short history of the agricultural landscape, people perceived agriculture as a contrast to “nature”.

These examples illustrate that valuation of cultural landscapes, from an aesthetical or emotional viewpoint, indeed may vary. People “read” the landscape in a way reflecting their own cultural

context [5]. Thus, irrespective of whether there exists any innate tendency among humans to appreciate certain landscape elements, the cultural context will affect how elements of the old cultural landscape are valued. What is evident, however, is that biodiversity *per se* is not a primary focus of local people's valuation of Swedish landscapes which still harbor a lot of semi-natural grasslands [100,110], but instead features related to beauty, heritage, identity of place, local involvement, and a "living landscape" (*i.e.*, a place where people can earn their living).

6. Conservation Models for Semi-Natural Grasslands

Conservation actions ultimately depend on how the society values different landscape structures and species. Maintenance and restoration are key actions for conservation. Such actions depend on "models" (or targets), that are based on some perception of a desired historical state. In Sweden, these models are usually inspired by late 19th or early 20th century landscapes. For example, the program for maintaining remaining semi-natural grasslands initiated during the 1980s in Sweden was much inspired by an interpretation of management during the late 19th century landscape as being "correct". Apart from noting that the choice of this particular time depth in itself was arbitrary, later research concluded that this management regime, which was based on a demand for a very high grazing pressure and removal of isolated trees and shrubs, was contra-productive from a biodiversity perspective (e.g., [55,111]). Furthermore, in a case study of conservation management in Sweden, Wästfelt *et al.* [112], noted a conflict between the farmers and the authorities concerning values, partly due to the fact that the model selected by authorities represented an arbitrary choice of an historical time when semi-natural grasslands were heavily over-grazed. Such a model was not only inappropriate for present-day farmers, it would also violate modern legislation of animal well-fare.

As illustrated by the interview studies performed in Sweden [100,108–110], several attributes related to history strongly influence local people's valuation of landscape features. Since the involvement of local stakeholders has become an increasingly important aspect of developing conservation programs [108,110,113], understanding landscape history and its impact on landscape features is a potentially strong motivator for conservation and thus the choice of appropriate models. Even if it is an open question whether there are innate human tendencies for appreciation of certain landscape features, or whether such preferences are just recent social constructs, an historical perspective of landscapes will provide a necessary basis for studies of valuation of semi-natural grasslands and landscapes including such grasslands. Perhaps the most important contribution from historical ecology is to "open our eyes" for the fact that choice of models for maintenance and restoration of semi-natural grasslands may be arbitrarily selected from a certain time-depth, and thus open for discussion. The preferred model may even be historically "incorrect" and representing what has been termed a "designed heritage" [20]. Whatever the resulting choice may be, it is important to gain insights of the historical background of current landscapes, the historical management procedures, and their impact on landscape features and biodiversity. To maintain and restore species richness in semi-natural grasslands in the future we need to find new management strategies and methods that mimic past labor intensive managements, but at the same time realize that we are never able to exactly reconstruct past landscapes.

7. Conclusions

The main conclusion we draw from this review is that an historical dimension is a necessary complement to the spatial dimension of a landscape perspective, for ecology and conservation biology, particularly when it comes to landscapes that have been integrated parts of human culture over a long time. The semi-natural grasslands in Sweden and the Baltic region cannot be understood without accounting for the history of the landscape where these grasslands are embedded. Even though we have focused on a particular habitat, located in a particular part of the world, the principal arguments for a historical landscape perspective are general and should apply to other habitats and regions as well. These arguments can be summarized as follows: (i) High biological diversity associated with semi-natural grasslands are the result of a species accumulation process that mechanistically is associated with the human management. A proper understanding of these mechanisms thus necessitates studies of how people have used and managed landscapes over a long period of time. The mechanisms relate to ecological processes, such as creation of habitats (niche space), niche shifts, dispersal and dynamics of species, due to the spatial configuration of various landscape elements; (ii) For conservation programs, studies in historical ecology are necessary to estimate the time-scale of species' response to landscape change, relating to the existence of an extinction debt and a colonization credit; (iii) Today many people appreciate and value landscapes including elements resulting from "old-fashioned" management, such as hay-making and grazing on semi-natural grasslands. This valuation is not only related to aesthetics, but also to emotions derived from a sense of identity, place and heritage. Understanding the emotional background (whether biologically inherent, or socially constructed) of these valuations assumes knowledge of the historical landscape development. Historical ecology has the potential to be an important motivator for conservation programs; (iv) Values related to an appreciation of historical landscapes, in addition to the direct values of biological diversity, constitute the rationale for conservation programs, and for societal costs associated with implementing these programs. To implement the conservation programs, there is a need to define models and goals for landscape related features, and management practices needed to achieve these goals. As we have illustrated, these models may in a sense be arbitrarily drawn from a range of alternatives emanating from different time periods back in history. They may even be recent constructs, representing a kind of "designed heritage". The main point we wish to make is to stress the importance of realizing that there are several options, and that a deep insight in landscape history is needed in order to inform the choices made, and the reasons for each particular option.

We will never be able to maintain or recreate exactly the same conditions that occurred previously during history. However, an informed perspective on landscape history, and how historical landscapes have been created by, and influenced, people and our associated biota, will be increasingly useful to alleviate any negative effects of ongoing changes in habitats and landscapes. Bringing this issue to light is an important task for research conducted from an historical landscape perspective.

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Author Contributions

OE and SAOC contributed equally to the content of this paper. OE did most of the writing, and SAOC made the figures.

Conflicts of Interest

The authors declare no conflicts of interest.

References

1. Lindborg, R.; Bengtsson, J.; Berg, Å.; Cousins, S.A.O.; Eriksson, O.; Gustafsson, T.; Hasund, K.P.; Lenoir, L.; Pihlgren, A.; Sjödin, E.; *et al.* A landscape perspective on conservation of semi-natural grasslands. *Agric. Ecosyst. Environ.* **2008**, *125*, 213–222.
2. Tschardtke, T.; Tylianakis, J.M.; Rand, T.A.; Didham, R.K.; Fahrig, L.; Batáry, P.; Bengtsson, J.; Clough, Y.; Crist, T.O.; Dormann, C.F.; *et al.* Landscape moderation of biodiversity patterns and processes—Eight hypotheses. *Biol. Rev.* **2012**, *87*, 661–685.
3. Driscoll, D.A.; Banks, S.C.; Barton, P.S.; Lindemayer, D.B.; Smith, A.L. Conceptual domain of the matrix in fragmented landscapes. *Trends Ecol. Evol.* **2013**, *28*, 605–613.
4. Schama, S. *Landscape and Memory*; Vintage Books: New York, NY, USA, 1995.
5. Antrop, M. Why landscapes of the past are important for the future. *Landsc. Urban Plan.* **2005**, *70*, 21–34.
6. Palang, H.; Spek, T.; Stenseke, M. Digging in the past: New conceptual models in landscape history and their relevance in peri-urban landscapes. *Landsc. Urban Plan.* **2011**, *100*, 344–346.
7. Balée, W. The research program of historical ecology. *Annu. Rev. Anthropol.* **2006**, *35*, 75–98.
8. Ellis, E.C.; Ramankutty, N. Putting people in the map: Anthropogenic biomes of the world. *Front. Ecol. Environ.* **2008**, *6*, 439–447.
9. Foster, D.R. Thoreau's country: A historical-ecological perspective on conservation in the New England landscape. *J. Biogeogr.* **2002**, *29*, 1537–1555.
10. Foster, D.R.; Swanson, F.; Aber, J.; Burke, I.; Brokaw, N.; Tilman, D.; Knapp, A. The importance of land-use legacies to ecology and conservation. *Bioscience* **2003**, *53*, 77–88.
11. Szabó, P. Why history matters in ecology: An interdisciplinary perspective. *Environ. Conserv.* **2010**, *37*, 380–387.
12. Vellend, M.; Brown, C.D.; Kharouba, H.M.; McCune, J.L.; Myers-Smith, I.H. Historical ecology: Using unconventional data sources to test for effects of global environmental change. *Am. J. Bot.* **2013**, *100*, 1294–1305.
13. Cousins, S.A.O.; Eriksson, O. The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. *Landsc. Ecol.* **2002**, *17*, 517–529.

14. Lindborg, R.; Eriksson, O. Historical landscape connectivity affects present plant species diversity. *Ecology* **2004**, *85*, 1840–1845.
15. Helm, A.; Hanski, I.; Pärtel, M. Slow response of plant species richness to habitat loss and fragmentation. *Ecol. Lett.* **2006**, *9*, 72–77.
16. Willis, K.J.; Gillson, L.; Brncic, T.M. How “virgin” is virgin rainforest? *Science* **2004**, *304*, 402–403.
17. Josefsson, T.; Bergman, I.; Östlund, L. Quantifying Sami settlement and movement patterns in northern Sweden 1700–1900. *Arctic* **2010**, *63*, 141–154.
18. Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: A Framework for Assessment*; Island Press: Washington, DC, USA, 2003.
19. Emanuelsson, U. *The Rural Landscape of Europe. How Man has Shaped European Nature*; The Swedish Research Council Formas: Stockholm, Sweden, 2009.
20. Storm, A. *Hope and Rust: Reinterpreting the Industrial Place in the Late 20th Century*; Stockholm Papers in the History and Philosophy of Technology; Royal Institute of Technology KTH: Stockholm, Sweden, 2008.
21. Riede, F. Adaptation and niche construction in human prehistory: A case study from the southern Scandinavian late glacial. *Philos. Trans. R. Soc. B* **2011**, *366*, 793–808.
22. Svenning, J.-C. A review of natural vegetation openness in north-western Europe. *Biol. Conserv.* **2002**, *104*, 133–148.
23. Lambeck, K. Shoreline displacement in southern-central Sweden and the evolution of the Baltic Sea since the last maximum glaciation. *J. Geol. Soc.* **1999**, *156*, 465–486.
24. Brandt, G.; Haak, W.; Adler, C.J.; Roth, C.; Szécsényi-Nagy, A.; Karimnia, S.; Möller-Rieker, S.; Meller, H.; Ganslmeier, R.; Friederich, S.; *et al.* Ancient DNA reveals key stages in the formation of central European mitochondrial genetic diversity. *Science* **2013**, *342*, 257–261.
25. Odgaard, B.V.; Rasmussen, P. Origin and temporal development of macro-scale vegetation patterns in the cultural landscape of Denmark. *J. Ecol.* **2000**, *88*, 733–748.
26. Welinder, S. Early farming households. In *The Agrarian History of Sweden from 4000 BC to AD 2000*; Myrdal, J., Morell, M., Eds.; Nordic Academic Press: Lund, Sweden, 2011; pp. 18–45.
27. *The Cultural Landscape during 6000 Years in Southern Sweden: The Ystad Project*; Ecological Bulletins 41; Berglund, B.E., Ed.; Munksgaard International Booksellers and Publishers: Copenhagen, Denmark, 1991.
28. Nielsen, A.B.; Giesecke, T.; Theurekauf, M.; Feeser, I.; Behre, K.-E.; Beug, H.-J.; Chen, S.-H.; Christiansen, J.; Dörfler, W.; Endtmann, E.; *et al.* Quantitative reconstruction of changes in regional openness in North-Central Europe reveal new insights into old questions. *Quat. Sci. Rev.* **2012**, *47*, 131–149.
29. Hannon, G.E.; Bradshaw, R.H.W.; Nord, J.; Gustafsson, M. The Bronze Age landscape of the Bjäre peninsula, southern Sweden, and its relationship to burial mounds. *J. Archaeol. Sci.* **2008**, *35*, 623–632.
30. Bradshaw, E.G.; Rasmussen, P.; Odgaard, B.V. Mid- to late Holocene land-use change and lake development at Dallund Sø, Denmark: Synthesis of multiproxy data, linking land and lake. *Holocene* **2005**, *15*, 1152–1162.

31. Kaplan, J.O.; Krumhardt, K.M.; Zimmermann, N. The prehistoric and preindustrial deforestation of Europe. *Quat. Sci. Rev.* **2009**, *28*, 3016–3034.
32. Pedersen, E.A.; Widgren, M. Agriculture in Sweden, 800 BC–AD 1000. In *The Agrarian History of Sweden from 4000 BC to AD 2000*; Myrdal, J., Morell, M., Eds.; Nordic Academic Press: Lund, Sweden, 2011; pp. 46–71.
33. Overland, A.; Hjelle, K.L. From forest to open pastures and fields: Cultural landscape development in western Norway inferred from two pollen records representing different spatial scales of vegetation. *Veg. Hist. Archaeobot.* **2009**, *18*, 459–476.
34. Poska, A.; Saarse, L.; Veski, S. Reflections of pre- and early-agrarian human impact in the pollen diagrams of Estonia. *Palaeogeogr. Palaeoclim. Palaeoecol.* **2004**, *209*, 37–50.
35. Reitalu, T.; Seppä, H.; Sugita, S.; Kangur, M.; Koff, T.; Avel, E.; Kihno, K.; Vassiljev, J.; Renssen, H.; Hammarlund, D.; *et al.* Long-term drivers of forest composition in a boreonemoral region: The relative importance of climate and human impact. *J. Biogeogr.* **2013**, *40*, 1524–1534.
36. Sköld, E.; Lagerås, P.; Berglund, B.E. Temporal cultural landscape dynamics in a marginal upland area: Agricultural expansions and contractions inferred from palynological evidence at Yttra Berg, southern Sweden. *Veg. Hist. Archaeobot.* **2010**, *19*, 121–136.
37. Alenius, T.; Mikkola, E.; Ojala, A.E.K. History of agriculture in Mikkeli Orijärvi, eastern Finland as reflected by palynological and archaeological data. *Veg. Hist. Archaeobot.* **2008**, *17*, 171–183.
38. Alenius, T.; Saarnosto, M.; Taavitsainen, J.-P.; Lunkka, J.-P. Records of land use and medieval settlement history in Vuonninen, Dvina Karelia, Northwest Russia. *Geoarchaeology* **2011**, *26*, 142–163.
39. Alenius, T.; Mökkönen, T.; Lahelma, A. Early farming in the northern boreal zone: Reassessing the history of land use in southeastern Finland through high-resolution pollen analysis. *Geoarchaeology* **2013**, *28*, 1–24.
40. Karlsson, H.; Emanuelsson, M.; Segerström, U. The history of a farm-shieling system in the Central Swedish forest region. *Veg. Hist. Archaeobot.* **2010**, *19*, 103–119.
41. Josefsson, T.; Gunnarsson, B.; Liedgren, L.; Bergman, I.; Östlund, L. Historical human influence on forest composition and structure in boreal Fennoscandia. *Can. J. For. Res.* **2010**, *40*, 872–884.
42. Austheim, G.; Eriksson, O. Plant species diversity and grazing in the Scandinavian mountains: Patterns and processes at different spatial scales. *Ecography* **2001**, *24*, 683–695.
43. Widgren, M. *Settlement and Farming Systems in the Early Iron Age: A Study of Fossil Agrarian Landscapes in Östergötland, Sweden. Stockholm Studies in Human Geography 3*; Almquist & Wiksell: Stockholm, Sweden, 1983.
44. Lagerås, P. *The Ecology of Expansion and Abandonment: Medieval and Post-Medieval Land-Use and Settlement Dynamics in a Landscape Perspective*; National Heritage Board: Stockholm, Sweden, 2007.
45. Nielsen, A.B.; Odgaard, B.V. Quantitative landscape dynamics in Denmark through the last three millenia based on the landscape reconstruction algorithm approach. *Veg. Hist. Archaeobot.* **2010**, *19*, 375–387.

46. Gadd, C.-J. The agricultural revolution in Sweden, 1700–1870. In *The Agrarian History of Sweden from 4000 BC to AD 2000*; Myrdal, J., Morell, M., Eds.; Nordic Academic Press: Lund, Sweden, 2011; pp. 118–164.
47. Cousins, S.A.O. Analysis of land-cover transitions based on 17th and 18th century cadastral maps and aerial photographs. *Landsc. Ecol.* **2001**, *16*, 41–54.
48. Flygare, I.A.; Isacson, M. The tension between modernity and reality. In *The Agrarian History of Sweden from 4000 BC to AD 2000*; Myrdal, J., Morell, M., Eds.; Nordic Academic Press: Lund, Sweden, 2011; pp. 214–256.
49. Cousins, S.A.O. Landscape history and soil properties affect grassland decline and plant species richness in rural landscapes. *Biol. Conserv.* **2009**, *142*, 2752–2758.
50. Dahlström, A.; Cousins, S.A.O.; Eriksson, O. The history (1620–2003) of land use, people and livestock, and the relationships to present plant species diversity in a rural landscape in Sweden. *Environ. Hist.* **2006**, *12*, 191–212.
51. Cousins, S.A.O.; Eriksson, O. After the hotspots are gone: Land use history and grassland plant species diversity in a strongly transformed agricultural landscape. *Appl. Veg. Sci.* **2008**, *11*, 365–374.
52. Luoto, M.; Rekolainen, S.; Aakkula, J.; Pykälä, J. Loss of plant species richness and habitat connectivity in grasslands associated with agricultural change in Finland. *AMBIO* **2003**, *32*, 447–452.
53. Pärtel, M.; Mändla, R.; Zobel, M. Landscape history of a calcareous (alvar) grassland in Hanila, western Estonia, during the last three hundred years. *Landsc. Ecol.* **1999**, *14*, 187–196.
54. Palmgren, E. Distribution of Semi-Natural Pastures in Sweden: A Comparison of Coverage Estimation Using Random Sampling and Total Registration Data Sets. M.Sc. Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden, 2010.
55. Vessby, K.; Söderström, B.; Glimskär, A.; Svensson, B. Species-richness correlations of six different taxa in Swedish semi-natural grasslands. *Conserv. Biol.* **2002**, *16*, 430–439.
56. *The 2010 Red List of Swedish Species*; Gärdenfors, U., Ed.; ArtDatabanken, SLU: Uppsala, Sweden, 2010.
57. Cousins, S.A.O.; Eriksson, O. Plant species occurrences in a rural hemiboreal landscape: Effects of remnant habitats, site history, topography and soil. *Ecography* **2001**, *24*, 461–469.
58. Gustavsson, E.; Lennartsson, T.; Emanuelsson, M. Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. *Biol. Conserv.* **2007**, *138*, 47–59.
59. Johansson, L.J.; Hall, K.; Prentice, H.C.; Ihse, M.; Reitalu, T.; Sykes, M.T.; Kindström, M. Semi-natural grassland continuity, long-term land-use change and plant species richness in an agricultural landscape on Öland, Sweden. *Landsc. Urban Plan.* **2008**, *84*, 200–211.
60. Reitalu, T.; Johansson, L.J.; Sykes, M.T.; Hall, K.; Prentice, H.C. History matters: Village distances, grazing and grassland diversity. *J. Appl. Ecol.* **2010**, *47*, 1216–1224.
61. Austrheim, G.; Olsson, E.G.A.; Grøntvedt, E. Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, Central Norway. *Biol. Conserv.* **1999**, *87*, 369–379.
62. Aggemyr, E.; Cousins, S.A.O. Landscape structure and land use history influence changes in island plant composition after 100 years. *J. Biogeogr.* **2012**, *39*, 1645–1656.

63. Eriksson, O. Species pools in cultural landscapes: Niche construction, ecological opportunity and niche shifts. *Ecography* **2013**, *36*, 403–413.
64. Poschlod, P.; Bonn, S. Changing dispersal processes in the Central European landscape since the last ice age: An explanation for the actual decrease of plant species richness in different habitats? *Acta Bot. Neerl.* **1998**, *47*, 27–44.
65. Auffret, A.G. Can seed dispersal by human activity play a useful role for the conservation of European grasslands? *Appl. Veg. Sci.* **2011**, *14*, 291–303.
66. Auffret, A.G.; Schmucki, R.; Reimark, J.; Cousins, S.A.O. Grazing networks provide useful functional connectivity for plants in fragmented systems. *J. Veg. Sci.* **2012**, *23*, 970–977.
67. Eriksson, O.; Cousins, S.A.O.; Bruun H.H. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *J. Veg. Sci.* **2002**, *13*, 743–748.
68. Eriksson, O.; Cousins, S.A.O.; Lindborg, R. Land use history and the build-up and decline of species richness in Scandinavian semi-natural grasslands. In *Pastoral Systems in Marginal Environments*; Milne, J.A., Ed.; Wageningen Academic Publishers: Wageningen, The Netherlands, 2005; pp. 51–60.
69. Öster, M.; Cousins, S.A.O.; Eriksson, O. Size and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. *J. Veg. Sci.* **2007**, *18*, 859–868.
70. Wilson, J.B.; Peet, R.K.; Dengler, J.; Pärtel, M. Plant species richness: The world records. *J. Veg. Sci.* **2012**, *23*, 796–802.
71. Berglund, B.E.; Persson, T.; Björkman, L. Late Quaternary landscape and vegetation diversity in a North European perspective. *Quat. Int.* **2008**, *184*, 187–194.
72. Berglund, B.E.; Gaillard, M.-J.; Björkman, L.; Persson, T. Long-term changes in floristic diversity in southern Sweden: Palynological richness, vegetation dynamics and land use. *Veg. Hist. Archaeobot.* **2008**, *17*, 573–583.
73. Pärtel, M.; Helm, A.; Reitalu, T.; Liira, J.; Zobel, M. Grassland diversity related to the late Iron Age human population density. *J. Ecol.* **2007**, *95*, 574–582.
74. Berg, Å.; Ahrné, K.; Öckinger, E.; Svensson, R.; Söderström, B. Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. *Biol. Conserv.* **2011**, *144*, 2819–2831.
75. Wretenberg, J.; Pärt, T.; Berg, Å. Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. *Biol. Conserv.* **2010**, *143*, 375–381.
76. Van Vuure, C. *Retracing the Aurochs: History, Morphology and Ecology of an Extinct Wild Ox*; Pensoft Publishers: Sofia, Bulgaria, 2005.
77. Eriksson, O. Regional dynamics of plants: A review of evidence for remnant, source-sink and metapopulations. *Oikos* **1996**, *77*, 248–258.
78. Johansson, V.A.; Cousins, S.A.O.; Eriksson, O. Remnant populations and plant functional traits in abandoned semi-natural grasslands. *Folia Geobot.* **2011**, *46*, 165–179.
79. Auffret, A.G.; Cousins, S.A.O. Past and present management influences the seed bank and seed rain in a rural landscape mosaic. *J. Appl. Ecol.* **2011**, *48*, 1278–1285.
80. Plue, J.; Cousins, S.A.O. Temporal dispersal in fragmented landscapes. *Biol. Conserv.* **2013**, *160*, 250–262.
81. Cousins, S.A.O. Extinction debt in fragmented grasslands: Paid or not? *J. Veg. Sci.* **2009**, *20*, 3–7.

82. Cousins, S.A.O.; Vanhoenacker, D. Detection of extinction debt depends on scale and specialization. *Biol. Conserv.* **2011**, *144*, 782–787.
83. Tilman, D.; May, R.M.; Lehman, C.L.; Nowak, M.A. Habitat destruction and the extinction debt. *Nature* **1994**, *371*, 65–66.
84. Cousins, S.A.O.; Ohlson, H.; Eriksson, O. Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. *Landsc. Ecol.* **2007**, *22*, 723–730.
85. Eriksson, Å. Regional distribution of *Thymus serpyllum*: Management history and dispersal limitation. *Ecography* **1998**, *21*, 35–43.
86. Eriksson, O.; Kiviniemi, K. Site occupancy, recruitment and extinction thresholds in grassland plants: An experimental study. *Biol. Conserv.* **1999**, *87*, 319–325.
87. Purschke, O.; Sykes, M.T.; Reitalu, T.; Poschlod, P.; Prentice, H.C. Linking landscape history and dispersal traits in grassland plant communities. *Oecologia* **2012**, *168*, 773–783.
88. Öster, M.; Ask, K.; Cousins, S.A.O.; Eriksson, O. Dispersal and establishment limitation reduces the potential for successful restoration of semi-natural grassland communities on former arable fields. *J. Appl. Ecol.* **2009**, *46*, 1266–1274.
89. Cousins, S.A.O.; Lindborg, R. Remnant grassland habitats as source communities for plant diversification in agricultural landscapes. *Biol. Conserv.* **2008**, *141*, 233–240.
90. Lindborg, R.; Eriksson, O. Effects of restoration on plant species richness and composition in Scandinavian semi-natural grasslands. *Restor. Ecol.* **2004**, *12*, 318–326.
91. Cousins, S.A.O.; Aggemyr, E. The influence of field shape, area and surrounding landscape on plant species richness in grazed ex-fields. *Biol. Conserv.* **2008**, *141*, 126–135.
92. Öster, M.; Ask, K.; Römermann, C.; Tackenberg, O.; Eriksson, O. Plant colonization of ex-arable fields from adjacent species-rich grasslands: The importance of dispersal vs. recruitment ability. *Agric. Ecosyst. Environ.* **2009**, *130*, 93–99.
93. The European Landscape Convention. Council of Europe. Available online: <http://www.coe.int/t/dg4/cultureheritage/heritage/landscape> (accessed on 10 March 2014).
94. Sweden's Environmental Objectives. Available online: <http://www.miljomal.nu> (accessed on 10 March 2014).
95. Orians, G.H.; Heerwagen, J.H. Evolved responses to landscapes. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*; Barkow, J.H., Cosmides, L., Tooby, J., Eds.; Oxford University Press: Oxford, UK, 1992; pp. 555–579.
96. Kaplan, S. Aesthetics, affect, and cognition: Environmental preference from an evolutionary perspective. *Environ. Behav.* **1987**, *19*, 3–32.
97. Pinker, S. The cognitive niche: Coevolution of intelligence, sociality, and language. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 8993–8999.
98. Boyd, R.; Richerson, P.J.; Henrich, J. The cultural niche: Why social learning is essential for human adaptation. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 10918–10925.
99. Whiten, A.; Erdal, D. The human socio-cognitive niche and its evolutionary origins. *Philos. Trans. R. Soc. B* **2012**, *367*, 2119–2129.
100. Stenseke, M. Biodiversity and the local context: Linking seminatural grasslands and their future use to social aspects. *Environ. Sci. Policy* **2006**, *9*, 350–359.

101. Buijs, A.E. Lay people's images of nature: Comprehensive frameworks of values, beliefs, and value orientations. *Soc. Nat. Resour.* **2009**, *22*, 417–432.
102. Fischer, A. On the role of ideas of human nature in shaping attitudes towards environmental governance. *Hum. Ecol.* **2010**, *38*, 123–135.
103. Van der Windt, H.J.; Swart, J.A.A.; Keulartz, J. Nature and landscape planning: Exploring the dynamics of valuation, the case of the Netherlands. *Landsc. Urban Plan.* **2007**, *79*, 218–228.
104. Greider, T.; Garkovich, L. Landscapes: The social construction of nature and the environment. *Rural Soc.* **1994**, *59*, 1–24.
105. Nassauer, J.I. Culture and changing landscape structure. *Landsc. Ecol.* **1995**, *10*, 229–237.
106. Bang, M.; Medin, D.L.; Atran, S. Cultural mosaics and mental models of nature. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 13868–13874.
107. Buijs, A.E.; Pedrolì, B.; Luginbühl, Y. From hiking through farmland to farming in a leisure landscape: Changing social perceptions of the European landscape. *Landsc. Ecol.* **2006**, *21*, 375–389.
108. Lindborg, R.; Stenseke, M.; Cousins, S.A.O.; Bengtsson, J.; Berg, Å.; Gustafsson, T.; Sjödin, N.E.; Eriksson, O. Investigating biodiversity trajectories using scenarios—Lessons from two contrasting agricultural landscapes. *J. Environ. Manag.* **2009**, *91*, 499–508.
109. Saltzman, K.; Head, L.; Stenseke, M. Do cows belong in nature? The cultural basis of agriculture in Sweden and Australia. *J. Rural Stud.* **2011**, *27*, 54–62.
110. Stenseke, M. Local participation in cultural landscape maintenance: Lessons from Sweden. *Land Use Policy* **2009**, *26*, 214–223.
111. Pihlgren, A.; Lennartsson, T. Shrub effects on herbs and grasses in semi-natural grasslands: Positive, negative or neutral relationships? *Grass For. Sci.* **2008**, *63*, 9–21.
112. Wästfält, A.; Saltzman, K.; Gräslund Berg, E.; Dahlberg, A. Landscape care paradoxes: Swedish landscape care arrangements in a European context. *Geoforum* **2012**, *43*, 1171–1181.
113. Kearney, A.R.; Bradley, G.A.; Petrich, C.H.; Kaplan, R.; Kaplan, S.; Simpson-Colebank, D. Public perception as support for scenic quality regulation in a nationally treasured landscape. *Landsc. Urban Plan.* **2008**, *87*, 117–128.