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Historical and Current Niche Construction in an Anthropogenic Biome: Old Cultural Landscapes in Southern Scandinavia

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Abstract: Conceptual advances in niche construction theory provide new perspectives and a tool-box for studies of human-environment interactions mediating what is termed anthropogenic biomes. This theory is useful also for studies on how anthropogenic biomes are perceived and valued. This paper addresses these topics using an example: "old cultural landscapes" in Scandinavia, i.e., landscapes formed by a long, dynamic and continuously changing history of management. Today, remnant habitats of this management history, such as wooded pastures and meadows, are the focus of conservation programs, due to their rich biodiversity and cultural and aesthetic values. After a review of historical niche construction processes, the paper examines current niche construction affecting these old cultural landscapes. Features produced by historical niche construction, e.g., landscape composition and species richness, are in the modern society reinterpreted to become values associated with beauty and heritage and species' intrinsic values. These non-utilitarian motivators now become drivers of new niche construction dynamics, manifested as conservation programs. The paper also examines the possibility to maintain and create new habitats, potentially associated with values emanating from historical landscapes, but in transformed and urbanized landscapes.

Keywords: biodiversity; conservation biology; landscape aesthetics; semi-natural grasslands; wooded meadows

1. Introduction

The Earth is now dominated by humans to such an extent that some authors have argued for a need to define "anthropogenic biomes" [1]. Anthropogenic biomes, also termed "anthromes" [2], represent the state of present vegetation cover better than traditionally recognized biomes for large portions of the Earth's surface. However, the whole idea may seem provocative for anyone who learned "classical" biomes, for example Heinrich Walter's Vegetation of the Earth [3], where biomes are characterized phytogeographically based on the structure of vegetation, as they are formed by climate impact, mainly temperature and precipitation. Based on the same kind of arguments as for anthropogenic biomes, many scholars argue that it is appropriate to recognize the Anthropocene as a new geological epoch. Apart from the stratigraphic problem of how to define this new epoch [4], the current controversies on anthropogenic biomes and the Anthropocene uncover deep disagreements on the underlying facts, the conceptual understanding of terms such as "nature" and "wilderness", how we perceive and valuate nature in a human-dominated world and, not the least, what would be the relevant goals and best options for conservation biology [5–13].

A relevant issue for this discourse on the relationships between humans and "wild nature" is the growing appreciation that organisms (including humans) and their environment are involved in reciprocal interactions. Organisms not only respond to environmental conditions, they also

modify their environment, and these modifications feedback to organisms, over time resulting in "ecological inheritance" and potentially micro-evolutionary change. Reciprocal organism-environment interactions are the focal topic of niche construction theory [14]. This theory has been particularly productive for studies of humans-environment interactions, variously termed human niche construction [15], cultural niche construction [16] or sociocultural niche construction [2]. For example, niche construction theory has been successful for understanding early domestication of plants and animals and the development of agriculture [17,18]. If reciprocal interactions between organisms and environment result in microevolutionary change, this implies that ecological and evolutionary time scales converge, providing a basis for eco-evolutionary dynamics [19–22]. Accordingly, human niche construction and eco-evolutionary dynamics are integral components of the formation and dynamics of anthropogenic biomes.

Whatever we think of it, it is a plain fact that a large part of the Earth's land surface is composed of cultural landscapes; a synonym is "domesticated landscapes" [23,24]. Often, these cultural landscapes are considered disturbed, degraded and constituting destroyed nature. However, particularly in parts of the world where cultural landscapes are rooted deeply in the social history of the region, these landscapes are indeed considered beautiful, and they are highly appreciated. In Europe, cultural landscapes are given high priority in conservation and planning [25] as evident from the European Landscape Convention [26], the first international treaty specifically concerned with landscape, with the aim of protecting, managing and planning European landscapes, even "ordinary" landscapes. Substantial financial support to maintain cultural landscapes is part of the European Common Agricultural Policy.

The goal with this paper is to use niche construction theory as a frame to examine the historical and current formation and dynamics of "old" historical cultural landscapes in southern Scandinavia (Figure 1). The meaning of "old" in this context will be explained below. Although this paper focuses on one particular kind of landscape in a specific geographic region, the conclusions should be general to many other cultural landscapes across the world. These Scandinavian landscapes are not wilderness, as they have been formed during millennia of human impact, thus obviously being anthropogenic. Landscapes that preserve what is regarded as historical features are regarded by many people as valuable, and they harbor a considerable diversity of wild species. Many species are currently declining, and elements of remaining old Scandinavian cultural landscapes that preserve features of historical management, such as hay-meadows, wood pastures, sea-shore meadows and open semi-natural pastures, are a high priority concern for conservation.

(**A**) (**B**)

Figure 1. *Cont.*

(**C**) (**D**)

Figure 1. Examples of old cultural landscapes in Sweden. (**A**) Managed wooded meadow with pollarded trees at Alvena, Province of Gotland. (**B**) Grazed oak landscape at Herröknanäs, Province of Södermanland. (**C**) Remnant of former cattle path leading through the infields to outlying pastures at Yttra Berg, Province of Halland. (**D**) Remnant pasture in a forest landscape at Stora Åsa, Province of Södermanland. Photos: The author.

In some recent papers, the historical development of cultural landscapes in Scandinavia has been examined from the perspective of human niche construction [27,28]. These studies constitute a starting point for this paper. Before summarizing them, I will briefly review the geographical and historical context of Scandinavian cultural landscapes and their current biodiversity. I then discuss current human niche construction focusing on two specific questions: (i) How does human niche construction today affect remnants of old historical cultural landscapes? (ii) Is it possible that "new" landscapes, formed by current niche construction, can be useful for preserving perceived values emanating from the old cultural landscapes?

2. Historical Context and Species Richness

Southern Scandinavia belongs to the nemoral (deciduous forest) zone in the south and the transitional boreo-nemoral zone, extending to the northerly boreal (coniferous forest) zone [29]. The forest cover in the boreo-nemoral zone is dominated by the two coniferous trees, Norway spruce (*Picea abies* (L.) H. Karst) and Scots pine (*Pinus sylvestris* L.), and birch (*Betula* spp.) and European aspen (*Populus tremula* L.), but various broad-leaved trees with a southern distribution, e.g., oak (*Quercus robur* L.), elm (*Ulmus glabra* Huds.), ash (*Fraxinus excelsior* L.) and lime (*Tilia cordata* Mill.), are frequently occurring. Large areas are used for agriculture and forestry. Much of what is presently forest has historically also been used for agriculture. Referring to suggested anthropogenic biomes [1] and excluding urban areas, southern Scandinavia would be classified either as "populated rainfed cropland" or as "populated forest".

Cultural landscapes in northern Scandinavia, for example transhumance systems with summer farms [30] or the Sami lands [31], will not be treated here. The historical development of cultural landscapes in southern Sweden has been treated in several studies [32,33]; see also [34] for a European perspective. A considerable fraction of the landscapes has been subjected to agricultural management during several millennia, in some areas since the introduction of agriculture in the fourth millennium BCE. Physical landscape structures that can be traced at least back to the first millennium CE (the Iron Age) are common, for example remains of grave fields, houses and byres, fence systems, such as stone walls, and land with a long uninterrupted history of management, such as hay-making [28]. Older structures occur, as well, but are less common. During the first centuries CE, land-use started to become organized into so-called infield systems [35,36]. Land around farms was enclosed to control herbivory

from livestock and was used as either cropland or meadows for the production of fodder for livestock, the latter covering the largest area. Moist or wet meadows were generally open, but dry meadows were often wooded and trees used for pollarding, i.e., harvest of leaves and twigs. Outside the enclosures, forests were used for grazing and collection of wood and other resources. Vast areas were used for harvesting of leaves and twigs from trees, used as fodder for livestock [37]. Over time, these forests developed into mixed semi-open woodlands. Although the causation behind the infield system is complex [28,38], the most reasonable rationale was the need for keeping the essential livestock over the cold winters. Broadly speaking and despite periods of reorganization of land ownership and tenure, this management system was maintained until the modernization of agriculture, which took place between the mid-19th century (in the most productive agricultural areas) and the early 20th century. In addition to the introduction of artificial fertilizers, livestock fodder now became produced on crop fields. Large areas of meadows were transformed to either cropland or forest, and outlying pasture land in semi-open forests was replaced by forestry focused on timber production [33].

The term "semi-natural grasslands" is currently used for various land types with a long management history, grazing or hay-making, incorporating both open and wooded grasslands, ranging from dry to mesic and wet, but not including cropland, which is ploughed and influenced by artificial fertilizers. Henceforth, "old" landscapes mean landscapes or landscape elements that can be traced back to a time before agricultural modernization when semi-natural meadow management and forest grazing were largely abandoned.

The transformation of the landscapes during the last 150 years is illustrated by a study from the Province of Södermanland, south of Stockholm [39]. Around the year 1900, semi-natural grasslands (including wooded areas) covered almost 50% of the landscape, and this figure is based on maps made after the first wave of major transition in meadow management (which in this province took place around 1860), suggesting that the historical extent of semi-natural grasslands was even larger. Today, there are around 500,000 hectares of semi-natural grasslands left in Sweden [33], of which around 100,000 hectares presently receive subsidies aimed at supporting biological and cultural values [40].

Semi-natural grasslands are generally species rich, particularly those that have been continuously managed for a long time [33]. For example, the density of plant species commonly exceeds 40 species/m^2 [41,42]. In addition to plants, these grasslands are hotspots for many different taxa [43], including fungi [44] and butterflies [45]. Large broad-leaved trees in semi-open woodlands are hotspots for epiphytic lichens [46] and insects [47]. Although birds generally respond to larger scale landscape patterns, many bird species are also associated with remaining elements of semi-natural grasslands [48].

Data from the Swedish 2015 red list [49] illustrate this diversity, but also that many species are declining. Of about 21,600 assessed species in Sweden, 19.8% (4273 species) are red-listed, and of these, a third, around 1400 species, are associated with agricultural landscapes. Abandonment of what is today considered traditional management (in practice, this often means cattle or sheep grazing) is a major threat. An additional mechanism behind species decline is that previous mosaic landscapes have been replaced by landscapes with only small and often isolated remnants of semi-natural grassland left, thus disconnecting habitats and preventing dispersal [50,51]. Thus, even if conservation management continues, populations experience a risk of local extinction, whereas colonization of previously unoccupied sites is unlikely.

3. Historical Human Niche Construction in Cultural Landscapes

Ecologists have long sought to explain the richness of wild species in European landscapes with a long history of human influence. One of the main questions has been whether pre-agricultural landscapes, even extending back over several glaciation-interglacial cycles during the Pleistocene, somehow resembled the cultural landscapes composed of small areas of cropland, open or wooded meadows and pastures and grassland-forest mosaics. If this is so, wild species would have been pre-adapted to the developing cultural landscapes. The mechanism behind this resemblance would have been for example grazing and browsing by wild herbivores [52] or disturbance caused by fires,

drought or running water [53]. This issue is still controversial. Some authors question whether the pre-agricultural landscape during the Holocene was at all open and suggest that closed forest dominated [54]. Other studies suggest that pre-agricultural Holocene landscapes were indeed relatively open, but that the mechanism was probably not herbivory [55]. Some recent studies have suggested that vegetation during previous interglacials may have been held open by large herbivores [56], so even if this were not the case during the Holocene, a species-pool adapted to open or semi-open habitats may have persisted from previous interglacials until the dawn of agriculture.

Niche construction theory may shed some new light on this issue. Between the Neolithic and pre-industrial times (i.e., before the modernization of agriculture described above), humans constructed niche space for numerous wild species, contributing to building a species pool that presently is associated with the old agricultural landscape dominated by open or semi-open grasslands and forest-grassland mosaics. This niche construction had four major components [27]: (i) forests were opened by clearing and burning; (ii) the created open/semi-open habitats were spatio-temporally stabilized by increasingly permanent human settlements; (iii) this stabilization promoted dispersal (particularly of plants) and local population persistence; (iv) due to harvesting hay-meadows, feeding harvested fodder to livestock and spreading livestock manure into cropland, the nutrient dynamics was altered so that fast-growing competitive plants were held back on land not used for crops. Meadows were extensive and cropland relatively small, so this effectively translocated nutrients from grasslands promoting species co-existence over large areas of semi-natural grasslands. Although elements of this niche construction may have been initiated along with the introduction of agriculture already from the fourth millennium BCE, all four components were strongly promoted by the introduction of infield systems in Scandinavia during the first centuries CE, i.e., the early Iron Age [28].

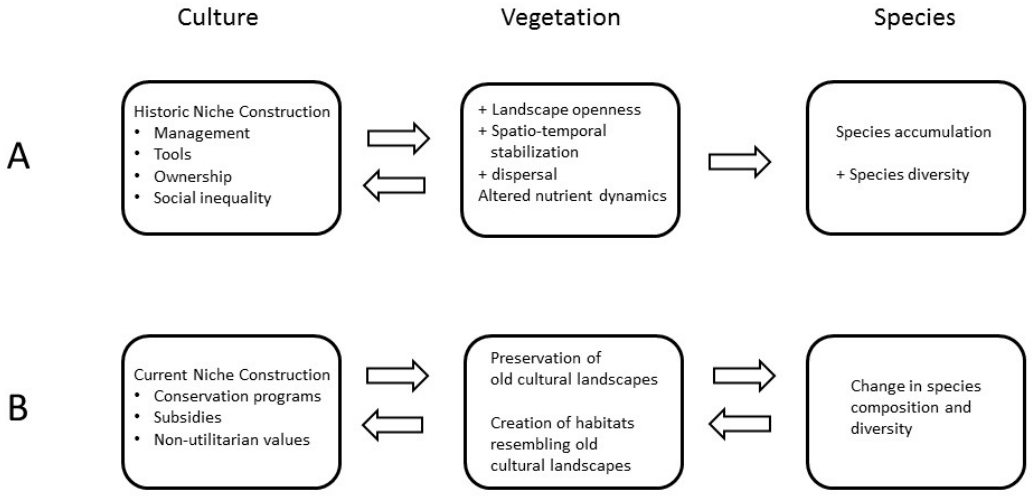

Figure 2. (**A**) Historical human niche construction forming the old cultural landscapes in Scandinavia [27]. (**A**) + indicates "increasing". (**B**) Current human niche construction influencing remnants of old cultural landscapes and new habitats resembling old cultural landscapes. The two-way arrows to/from "Species" in (**B**) reflect that species composition and diversity affect conservation programs and current valuation of landscapes. See the text for an explanation.

In this model of historical niche construction (Figure 2A), there is no need for pre-agricultural vegetation analogs harboring the species composition and high diversity we now know from semi-natural grasslands. What is sufficient is that there existed at least small areas of open/semi-open vegetation somewhere in the pre-agricultural landscape, each of them harboring subsets of the species pool later associated with managed land. Based on the analyses of pre-agricultural vegetation in northern Europe, this is highly likely [53,55]. As a side-effect, the above-mentioned mechanism resulted in "species accumulation" in the infields and their outlying pasture land, i.e., managed habitats in the

vicinity of farms and small villages. As species accumulated, species interaction networks became more complex (pollinating insects, herbivores, seed dispersing animals). The niche construction process may also have included shifts in realized niches, enabling forest species to expand into grasslands, and potentially eco-evolutionary dynamics altering fundamental niches [22,27]. However, conclusive evidence of such niche shifts is lacking, so this remains speculative.

The process involved feedback relations to human culture, thus being properly labelled as human niche construction. Many features of human culture may have been affected by the infield systems, e.g., management procedures, tools, perceptions of land ownership and social inequality [28]. These changes contributed to promoting the ecological niche construction by expanding the area of meadows and pastures and, associated with the development of "private" land ownership, also the spatiotemporal stabilization of managed land [28].

In his overview of ecology in an anthropogenic biosphere, Ellis [2] suggested some general trends in land use and species diversity for a hypothesized temperate woodland biome, associated with four "socioecological systems" ("hunter gatherer", "horticultural", "agrarian" and "industrial"). The historical human niche construction described here for the period from the early Iron Age until the modernization of agriculture during late 19th century corresponds to the "agrarian" phase in Ellis' Scheme 2, Figure 5. However, in Ellis' Figure 5C, pasture decreases and cropland increases. This was not true for Scandinavian cultural landscapes. As explained above, semi-natural grasslands were used as hay-meadows (and for pollarding of trees), and outlying land, mainly wood pastures, was totally dominating in area. Crop fields were relatively small. Estimates based on cadastral maps from the 17th and 18th centuries suggests that crop fields covered less than 20% of the infield area [33]. In this estimate, the extensive wood pastures outside the fenced infields is not included, leading to the conclusion that crop fields made up just a few percent of managed land. In Ellis' Figure 5E, native plant species richness declines during the agrarian phase. This is not the case for Scandinavian cultural landscapes. Studies of long-term trends suggest an increased local species richness associated with agricultural expansion [57], and remaining pastures and meadows with a long management history are exceptionally species rich [33]. A study from Estonia showed that there is a strong positive correlation between present-day plant species richness and estimated human population density during the late Iron Age, around 1000 years ago [58]. Moreover, the landscape was heterogeneous, creating habitats for numerous wild species [34,59]. There is no evidence suggesting that the transformation of the original forests was associated with species extinctions. The species that probably were most affected negatively were large carnivores that were hunted as they threatened the livestock (e.g., grey wolves, brown bears, Eurasian lynx). In Sweden, and indeed across Europe, these large carnivores are still maintained in modern landscapes [60], although grey wolves have been close to becoming extinct in Sweden.

Consequently, human niche construction associated with the "agrarian" phase, until the modernization of agriculture, was not only compatible with maintaining a high native species diversity, it promoted species density in the landscapes. These highly diverse and species-rich landscapes now constitute the baseline for the modern society's assessment and valuation of trends in species richness. This baseline is thus an anthropogenic landscape, strongly influenced by humans during several millennia, and where the properties of vegetation (openness, species composition and density) are a result of human niche construction, a process that also included feedbacks to human culture, for example management practices and the perception and regulations of land ownership.

4. Current Human Niche Construction Affecting Old Cultural Landscapes

In the synthesis of the extensive and pervasive impacts of the human society on the biosphere, Ellis [2] outlined an "anthroecology theory" based on the premise that the ecological patterns, processes and dynamics of the present day, past and foreseeable future are shaped by human societies. Some features of this theory (and the suggested approach for ecological research) are relevant for the question of how current niche construction affects the remains of the old Scandinavian cultural

landscapes. Firstly, the baseline is anthropogenic. As described above, the landscape, vegetation, species composition and diversity of plant and animal communities have been formed by management over a long time. Secondly, people have to be incorporated. In cultural landscapes, exclusion of human impact would be pointless [61]. The drivers that shape these landscapes are societal, as are the values assigned to, for example, remaining species-rich semi-natural grassland. Thirdly, "pedagogy is destiny" ([2]; p. 319). In order to manage and appreciate historical elements in landscapes, knowledge of historical landscape ecology and how current management relates to this history will be essential [25,62–64].

The examination of how old Scandinavian cultural landscapes are affected by current human niche construction focuses both on the actual remnants of these landscapes (for example, remaining managed meadows and pastures) and "new" landscapes that may somehow mimic features of old cultural landscapes. It is important to keep in mind that in order to be a niche construction process, there has to be reciprocal interactions between the niche constructing agents (humans) and the species whose niches are affected and, in turn, back to the niche constructing agent. In other words, the effects caused by a set of activities, for example a certain management influencing vegetation structure and species richness, should feedback to the activities, leading to a revision of management. The human activities (including how the effects of these activities are perceived and valued) can be regarded as a reflection of "culture", which over time changes in response to the interaction. Likewise, the interaction affects components of the environment, such as vegetation structure and species richness, which thus also change over time.

4.1. Utilitarian and Non-Utilitarian Motivators for Maintaining Old Cultural Landscapes

Historically, the ultimate driver creating the cultural landscapes, the infield systems with their hay-meadows and crop fields and the outlying land dominated by wood pastures, was the need for producing the necessities for people's livelihood. For the remaining old cultural landscapes today, we must recognize that the drivers are totally different. First and most obvious, there are international agreements that ratifying nations (such as Sweden) are obliged to follow, for example the Convention of Biological Diversity and The European Landscape Convention. However, referring to high-level policy decisions does not really answer the question why (and how) people in modern societies at all care for landscape features associated with old historical landscapes.

To tackle this question, one may distinguish between utilitarian and non-utilitarian motivators of conservation (although the distinction is not absolutely clear). These two approaches sometimes are regarded as conflicting [12], but could, some argue, complement each other [9,65]. The concept of ecosystem services [66] is the most common way to approach the valuation of nature and has become a major approach for motivating biodiversity conservation [67]. Ecosystem services are based on a mainly utilitarian framework, but also incorporate components that are not directly utilitarian ("cultural ecosystem services").

Studies of utilitarian ecosystem services related to remaining old cultural landscapes in Sweden have yielded quite vague results. There is a market in Sweden for meat production labelled as "semi-natural grassland meat" (more expensive than "ordinary" meat), although any benefits concerning health and taste for consumers are contentious. There is a general understanding that heterogeneous landscapes (e.g., including remnant of meadows, pastures and grassland-forest mosaics) promote biodiversity and thereby indirectly ecosystem services associated with this diversity [68], such as pollination [69]. However, although a diverse and heterogeneous landscape may indeed promote various ecosystem services such as pollination, it is unclear whether the existence of remnant old cultural landscape habitats is essential for these ecosystem services or whether "new" diverse and heterogeneous landscapes would suffice equally well. Indeed, a thorough analysis of multifunctional bundles of ecosystem services incorporating urban, agricultural and forest environments in Sweden revealed few benefits that could be directly related to remnants of old cultural landscapes [70].

Instead it is likely that non-utilitarian motivators are the strongest and most relevant societal drivers for preserving features of the old cultural landscapes. As described above, these landscapes are species-rich, and many species are declining. In addition to obligations following from Swedish ratification of international conventions, a sense of valuing species "for their own sake", i.e., their intrinsic value, is contributing to motivate the preservation of species-rich landscapes. However, for most people, an interest in rare plants, fungi and insects is likely to be quite limited, and even for the farmers actually managing the semi-natural pastures and meadows, other motivators are more important. Interview studies conclude that continuing subsidies for keeping grazing regimes are essential, but foremost, these studies suggest that values related to "beauty", "place and identity" and "cultural heritage" are the strongest motivators [71,72]. As remarked by Antrop ([25]; p. 21): " . . . the ability to tell the history of a place strongly enhances the identity and the overall value." Generally, aspects of beauty, identity and heritage are essential ingredients for how people perceive and valuate landscapes [73].

The European Landscape Convention [26] defines landscape as "an area, as perceived by people, whose character is the result of the action and interaction of natural and/or human factors" (Article 1a), and landscape protection means "actions to conserve and maintain the significant or characteristic features of a landscape, justified by its heritage value derived from its natural configuration and/or from human activity" (Article 1d). A key term here is "heritage". Heritage is a contested concept. Some scholars consider heritage (at least partly) as a social construct, its meaning being continuously negotiated in the context of present societies [74–76]. One study suggested that heritage is produced as people "experience, assign meaning to and act upon local landscape features" [77]. Heritage refers to some perceived baseline, placed somewhere in the past. In the case of the old cultural landscape we discuss here, this baseline is often what can be documented on cadastral maps from the 18th–19th centuries and interpretations of what is observed presently at sites where the historically documented management has been maintained. Even if such baselines are somehow arbitrary, they serve as models for conservation management and restoration.

A common theme in the discourse on landscape values is landscape aesthetics [73], and this aspect repeatedly is stressed in interview studies as a strong motivator for preserving features associated with old cultural landscapes [71,77,78]. Evolutionary psychologists have attempted to understand people's preferences for landscapes by considering them as potentially adaptive, for example the "savanna hypothesis" [79] proposing that humans would have an evolved preference for semi-open, resource-rich habitats (rich in flowers and fruits, rich in game species, with available water, etc.) providing food and protection. Kaplan [80] suggested that preferred landscapes are characterized by an intermediate degree of complexity. Although these ideas have received some support [81], they may seem too simplified and culturally biased, and it remains speculative whether humans at all have any inherent tendency to experience specific landscape features as beautiful. Whatever the underlying mechanisms are behind perceptions of landscape beauty, perceived aesthetic values are a contributing driver for how people and society influence species and landscapes. Furthermore, features of these landscapes, for example vegetation structure and species richness, feedback to perceived landscape aesthetics. This reciprocal interaction opens a possibility of using niche construction theory for research in evolutionary aesthetics [82], a largely unexplored research field.

This brief overview of how remaining features of the old cultural landscapes are valued in the present-day society suggests that utilitarian motivators are relatively weak in comparison to non-utilitarian motivators related to species' intrinsic value, landscape beauty and heritage. Direct utilitarian benefits (particularly those that can be measured monetarily) are likely to be small.

4.2. Effects of Current Niche Construction on Remaining Old Cultural Landscapes

As the drivers that created old cultural landscapes have been replaced by mainly non-utilitarian drivers manifested as conservation and restoration programs, the ecological effects on species composition and richness have also changed. Table 1 and Figure 2B summarize these changes.

First and foremost, the previous dominance of managed semi-natural grasslands (infield meadows, outlying pasture land) has been replaced by the dominance of production forest and crop land. Remaining semi-natural grasslands are small and isolated. One of the main effects of the historical niche construction process was species accumulation due to the existence of spatio-temporally-stable large tracts of managed grassland and grassland-forest mosaics, promoting both population colonization and persistence [27]. In the current landscape, populations in remaining fragments of semi-natural grasslands are subjected to a risk of local extinction without having the possibilities of re-colonization (or rescue effects). Dispersal in the historical landscape was promoted by the large area and high connectivity of managed land and by the movement of livestock and hay [51,83]. Today, dispersal is restricted, although some new dispersal agents (e.g., vehicles) may promote dispersal along linear landscape elements, such as roads [84]. Thus, species richness will decline, although there may be a considerable time-lag in the extinction process, resulting in an extinction debt [33,50,85]. Secondly, the management guided by conservation goals deviates from the historical management, for example concerning grazing and mowing intensity and timing, and variability in management among years [86,87]. Although the long-term consequences of this conservation-driven management are not well known, it is probable that it will also in the long run reduce species richness. Thirdly, new and competitive species colonize semi-natural grasslands as a result of propagule pressure from surrounding and now dominating vegetation, e.g., production forests and fertilized grassland [88]. Some of these species are non-natives (e.g., *Lupinus polyphyllus* Lindl.) [89]. Although incoming species are still regarded as a minor problem in comparison with the abandonment of management, these species are likely to be increasingly common in remaining old cultural landscapes in the future.

Table 1. Features of current niche construction affecting present-day remnants of old cultural landscapes. Each of these features constitutes a change in relation to the historical niche construction with implications for species composition and richness.

Components of Current Niche Construction	Comparison with Historical Niche Construction	Effects on Species Composition and Richness
Landscape configuration	• Transformation of grasslands and forests due to new forms of management. • Remaining semi-natural grasslands small and isolated.	• Reduced population colonization. • Increased risk of local population extinction. • Extinction debt and reduced species richness.
Dispersal	• New dispersal agents: Humans and vehicles have replaced livestock and hay. • Existing dispersal pathways linear (e.g., road verges).	• Reduced population colonization.
Management	• Guided by subsidies and conservation programs. • Grazing and mowing regimes deviating from historical management.	• Increased risk of local population extinctions?
Inflow of species from dominating vegetation, and non-native species	• Species-pool altered.	• Species composition changes. Effects on species richness unknown.

The niche space constructed by historical human niche construction has become altered and replaced by new niche constructing processes, which in the long term will alter the species-pool associated with the remaining old cultural landscape. Although conservation management may be successful in maintaining remnants of the old cultural landscape structurally, for example as well-managed pastures or wooded meadows with large deciduous trees, the overall changes that concern the whole "new" cultural landscapes will ultimately and unavoidably alter the species pool. The large number of red-listed species associated with the agricultural landscapes, mentioned above, is a reflection of these changes in human niche construction.

4.3. New Landscapes Mimicking Features of Old Cultural Landscapes

The remaining area of semi-natural grasslands is small. This means that the ordinary everyday landscape experienced by most people does not include such areas, although traces such as individual old trees, sometimes with signs of previous pollarding, may be encountered. Although ordinary present-day agricultural landscapes are generally less diverse biologically as compared to old cultural landscapes [90], interview studies suggest that even such landscapes, transformed by modernization, may be highly valued and appreciated by people [72]. One study concluded that people in Sweden often regard agricultural landscapes as "nature" [91]. It is beyond the scope here to examine such a conceptual understanding of nature, but it is obvious that this nature concept is totally different from the idea of "wilderness" that dominates the American discourse on nature [12,92].

One may ask if modern landscapes over time may produce similar aesthetic values (and perhaps species richness) now associated with old cultural landscapes. One may also ask whether new habitats over time, if they are maintained, will evoke similar feelings of heritage as old cultural landscapes. Another way to phrase this question is: Can values, originally deriving from the old cultural landscapes, thus perceived as beautiful and representing a valuable heritage, be transferred to landscape elements that are not "authentic" old cultural landscapes. The concept of authenticity is problematic, however. The social motivation for historical management (a necessity for people's livelihood) has been replaced by drivers that emanate from either high-level policy decision (e.g., subsidies from the European Union) or non-utilitarian cultural phenomena, such as perceptions of beauty and heritage. We may have no direct evidence of how farmers up till the 19th century felt about their landscapes, but it seems unlikely that beauty was an important driver behind management practices. In fact, existing documentation from the early 20th century [93] suggests that historical hay-meadow harvesting was so exhausting physically that it seems more likely that the farmers considered hay-meadows as awkward. Thus, although the physical location of a semi-natural grassland where old cadastral maps confirm a long uninterrupted management confers "authenticity of place", old cultural landscapes are obviously not authentic socio-ecologically. This holds also to some extent for their actual vegetation structure. The ecological effects of current conservation management are unavoidably different from what was achieved by the historical management [28,86,87,94]. These problems should not be understood as an excuse for downgrading the value of maintaining and restoring sites with a long history of grazing and mowing management, but only to stress the complexity of using "authenticity" as a valuation criterion for landscapes.

Below are three examples of "new habitats" (cf. "novel ecosystems" [5]) created in modern landscapes, which may contribute to maintaining features from old cultural landscapes:

(1) The area and connectivity of semi-natural grasslands may be extended using ex-arable fields. These fields are former crop fields, thus subjected to previous ploughing and fertilization, which have been recently transferred to pastures. Initially, they are species poor, but over time, they are colonized by plants typical for semi-natural grasslands [95]. Seed sowing may speed-up the process [96]. Ex-arable fields are not likely to reach the same species composition and density as well-managed semi-natural grasslands [95], but they may approach a considerable diversity. If ex-arable fields have not been too heavily fertilized previously, they will, for most people, appear indistinguishable from semi-natural grasslands, and they will contribute to maintaining

a generally open landscape, rich in flowers and associated insects. In addition to considerably increasing the grazed area and the connectivity among grazed areas, these grasslands also have the advantage of being more profitable economically, thus increasing the likelihood that farmers will maintain the grazing regime [97]. Thus, by applying a landscape perspective, one may maintain features of the old cultural landscapes even within a modern landscape matrix [78,98].

(2) Road verges and other constructed linear grassland landscape elements, if properly managed, may harbor plant species otherwise dependent on semi-natural grasslands and grassland-forest mosaics [99] and enhance the dispersal of these species [84]. Such linear grasslands have also been found favorable for butterflies [45,100]. However, road verges are also favorable for several invasive plants, for example lupines (*Lupinus polyphyllus*). Lupines are often regarded as beautiful when flowering along the motor-ways. Their ecological effects are more controversial. As they may develop mono-specific stands, lupines may be negative for native flora [89]. However, their massive flower production may also have positive effects on pollinators, such as bumble-bees, and thereby also on the pollination of other plants [101]. Road verges undoubtedly open space for the development of new plant communities, but it is still an open question how these communities will be perceived and valuated in the future.

(3) Park landscapes may hold considerable biological and aesthetic qualities and may function as refuges for a range of temperate forest species [102,103]. Species diversity is dependent on the age of the park, however, suggesting that if recently created, the park landscapes may need extensive time periods to reach their potential as diversity hotspots. Even though the parks that currently have high diversity are old, they were once created, and there is no practical limitation to create new park landscapes. A long-term management strategy will thus be needed in order to utilize parks for this purpose. As the fraction of urban woodland in Swedish cities is on average 20% of urban area [104], there is a potential for creating biologically diverse landscapes even in strongly transformed landscapes.

5. Conclusions

This paper examined human-environment interactions in landscapes that have for long been utilized and shaped by humans, thus being part of an anthropogenic biome. The rationale behind the choice of old cultural landscapes in southern Scandinavia as the study object was that these landscapes are currently highly valued due to their beauty and biological richness, much in the same way as is "wilderness" in other parts of the world. The approach used was based on niche construction theory. As suggested by Odling-Smee et al., ([105]; p. 22): " ... the practical study of ecology and evolution is not changed by this perspective (...). What is different is the focus of investigation." One may thus see niche construction theory as a tool-box for explicitly considering dynamic interactions between the organisms in focus of studies and their surrounding biotic and abiotic environments. When humans are key actors in these interactions and cultural phenomena are involved, the concept used is human niche construction [15] focusing on elements of human culture that affect and are affected by the properties of the surrounding nature. Likewise, one needs to identify features of the surrounding nature that are affected by the cultural impacts; these features are resulting from the creation, modification or destruction of species' niches. Over time, this interaction alters both culture and nature.

One issue was how human niche construction today affects remnants of the historical old cultural landscapes in southern Scandinavia (Figure 2B). The main conclusion is that current niche construction is driven by mechanisms based mainly on non-utilitarian motivators. Features produced by historical niche construction, landscape composition and species richness are in the modern society reinterpreted to become values associated with beauty and heritage and species' intrinsic values. These values now become drivers of new niche construction dynamics, manifested as conservation programs. However, the conservation management is only partly similar to historic management, for example differing in grazing and mowing intensity, timing and variability. This, together with the consequences of remnant

old cultural landscapes being generally small and isolated, implies that biological features such as species composition and richness will unavoidably change.

A second issue was whether it is possible that "new" landscapes, formed by current niche construction (i.e., not only niche construction following from conservation), can be useful for preserving perceived values emanating from the old cultural landscapes. This issue concerns landscape features that are not "authentically" rooted in historical management, but due to their biological properties, may resemble old cultural landscapes. Based on the realization that concepts such as "beauty" and "heritage" to some extent are constructed and negotiated in the context of the modern society, one may hypothesize that similar values that are associated with old cultural landscapes can be transferred to new landscapes. This is admittedly controversial, and there has not been much research useful to examine this hypothesis. Some authors fear that such a "transfer of values" may lead to a "shifting baseline" eventually eroding the biological values originally aimed for protection [106]. There is some evidence that new habitats, such as ex-arable fields, road verges and urban parks, to some extent may harbor species formerly associated with old cultural landscapes. However, whether such habitats over time may be assigned values related to heritage and aesthetics is an open question. However, results from interview studies suggest that people's appreciation of landscapes is much related to the fact that the landscape is inhabited, harbors agriculture and has the capacity to sustain people's living [71,72,91]. This indicates that values related to heritage continue to be produced [77].

This essay may have produced more questions than it answers. Several research topics are still poorly explored. Firstly, the long-term effects on species of current conservation management in remnants of old cultural landscapes is not adequately known, and the same holds for the potential of "new" habitats for preserving species associated with the old cultural landscape. Thus, properly-designed long-term studies should be promoted. Secondly, if the conclusion is correct that a key to maintain old cultural landscapes is perceptions of aesthetics and cultural heritage, it would be highly interesting to examine how these concepts interact with biological features in changing landscapes. Such research is essential to inform how current landscape transformation and the creation of new landscapes will be perceived and valued in the future.

As a final remark, I return to the controversies surrounding anthropogenic biomes and conservation biology, referred to in the opening paragraph of this paper [5–13]. Kareiva and Marvier [6] can be used as a representative of (what critics call) "new conservation science". The basic arguments in this suggested re-orientation of conservation biology (which Kareiva and Marvier term conservation science) can be summarized as follows: (i) ecological dynamics cannot be separated from human dynamics; (ii) conservation science has a goal to develop strategies to maximize benefits to both people and biodiversity, and conservation will be successful only if people support conservation goals; (iii) conservation must occur within human-altered landscapes, since there exists no "pristine" nature; (iv) ecosystem services are a major motivation for conservation; (v) conservation should be optimistic, not only because of a trust in the potential for wise societal decisions, but also because nature is more resilient than usually believed.

The critique of new conservation science has been forceful [7,11,12] and can be summarized as follows: (i) new conservation science promotes a human-centered ethic and neglects the intrinsic value of nature; (ii) new conservation science puts too strong a focus on people's self-interest expressed as economic values, instead of social and moral values, a "self-centered dogma (. . .) ingrained in neoliberal economic theory . . . " ([11]; p. 509); (iii) new conservation science falls into the abyss of "social constructivism", in particular by claiming that nature (wilderness) is a social construct and does not exist; (iv) new conservation science is overly and naively optimistic about our capacity of stewardship for nature.

Remaining old cultural landscapes in Scandinavia are highly diverse biologically, and despite being anthropogenic, they not only host numerous wild species, but are also generally considered as valuable. These values are manifested both in high-level policy (e.g., the European Landscape Convention), by large transfers of subsidies to farmers maintaining what is perceived as important

remnants of these landscapes and in people's appreciation of landscape beauty and heritage. This valuation is however not a reflection of "self-interest" or "neoliberal economic theory". My conclusion is that utilitarian ecosystem services play a very subordinate role in this valuation. On the contrary, intrinsic values, referring both to species, but even to structural features of landscapes, a still managed wooded meadow or a species-rich pasture placed on land that has been used uninterruptedly since the Iron Age, are clearly more important. Utilitarian ecosystem services are not a major motivation for the conservation of these landscapes. Thus, being anthropocentric does not exclude intrinsic values. Furthermore, although components of nature, such as "wild" species inhabiting cultural landscapes, simply exist irrespective of human's perceptions of them, we should recognize that the perceptions per se of beauty, heritage and authenticity partly are social constructions. This does not, however, downgrade these perceptions and values, but rather forces us to promote research forwarding our understanding of how people experience and value nature.

In fact, none of these opposing opinions seem to accurately reflect the situation for the landscapes examined here. In a recent paper, Mace [9] outlined different views of conservation from the early 1960s until today. She concluded that an early view, "nature for itself" (stressing wilderness and species intrinsic values) is largely compatible with a view "people and nature" (stressing the interdependence of people and nature, environmental change and adaptability) and that these views are in fact not so different from each other as they at first may seem. This conclusion is supported by the examination of historical and current niche construction dynamics of old Scandinavian cultural landscapes.

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