Pitkänen, Timo (1), Mussaari, Maija (2) and Käyhkö, Niina (1)

Assessing restoration potential of seminatural grasslands by landscape change trajectories

- (1) University of Turku, Department of Geography and Geology, Geography Division, FI-20014, Turku, Finland
- (2) Metsähallitus Natural Heritage Services, Kärsämäentie 8, FI-20300, Turku, Finland

Corresponding author: Timo Pitkänen

E-mail: <u>timo.pitkanen@utu.fi</u> Phone: +358 2 333 6059 (office) or +358 40 963 7444 (mobile) Fax: not available

Abstract

Species rich semi-natural grasslands have rapidly declined and become fragmented in Northern Europe due to ceased traditional agricultural practices and animal husbandry. Restoration actions have been introduced in many places to improve the habitat conditions and increase the area to prevent any further losses of their ecological values. However, given the limited resources and long time span needed for successful restoration, it is essential to target activities on sites having a suitable initial state and where the effects of restoration are most beneficial for the habitat network. In this paper we present a conceptual framework for evaluating the restoration potential of partially overgrown and selectively managed semi-natural grasslands in a moderately transformed agricultural environment in south-western Finland. On the basis of the spatio-temporal landscape trajectory analysis, we construct potential restoration scenarios based on expected semi-natural grassland characteristics that are derived from land productivity, detected grassland continuum and date of overgrowth. These scenarios are evaluated using landscape metrics, their feasibility is discussed and the effects of potential restoration are compared to the present extent of open semi-natural grasslands. Our results show that landscape trajectory analysis and scenario construction can be valuable tools for the restoration planning of semi-natural grasslands with limited resources. The approach should therefore be considered as an essential tool to find the most optimal restoration sites and to pre-evaluate the effects.

KEYWORDS

Semi-natural grassland, biodiversity, landscape change, habitat fragmentation, restoration, GIS

Semi-natural grasslands are habitats dominated by indigenous species with a structure and composition affected by long-term human influence. They have been maintained by cultivation and animal husbandry, and in northern Europe are characterized by low productivity but high species diversity (Ihse 1995; Vainio et al. 2001; Cousins and Eriksson 2008). It is estimated that these grasslands have existed in northern Europe for thousands of years and have been sustained in their semi-natural condition until recent times (Eriksson et al. 2002). However, given the long time span required for evolution and specification, plant species specialized to these environments must have already been present before the dawn of human intervention. It has been suggested that the influence of large herbivorous mammals at least since 1.8 million years, in addition to other factors such as fire and floods, maintained a continuum of the grassland habitats with variable extent until a few millennia ago, thus initially supporting plant species' adaption into moderate disturbances (Pärtel et al. 2005; Whitehouse and Smith 2004; Svenning 2002). After the extinction of these megaherbivores and more efficient prevention of other disturbing processes, similar effects have been mitigated by traditional, extensive agriculture (Pykälä 2000b).

In the era of extensive traditional agriculture, livestock keeping required large areas of semi-natural grasslands in northern Europe. They provided important grazing resources in the summer and enabled the collection of hay to feed the cattle during the winter (Robertson et al. 1990; Lindgren 2000; Luoto et al. 2003; Pykälä 2000a). In addition to foraging, leaf harvesting and coppicing were also used in many regions to maximize fodder production on partly open semi-natural grasslands (Slotte 2001). Scale and intensity of the agriculture had some fluctuations but in general, the land use regime lasted until the early decades of the 1900s. After that, however, changes in agricultural practices led gradually to the abandonment of small-scale animal husbandry which caused major consequences for semi-natural grasslands. It was no longer profitable to use semi-natural grasslands for extensive fodder production but instead many of them

were changed into intensively cultivated and fertilized fields, or were abandoned and afforested (Robertson et al. 1990; Eriksson et al. 1995; Ihse 1995; Luoto et al. 2003; Hannus and von Numers 2010).

Within a relatively short time, this development led to a simplified landscape structure and reduced connectivity of the semi-natural grassland patches, with detrimental consequences to the reproduction and survival of species (Cousins and Eriksson 2002; Luoto et al. 2003; Lunt and Spooner 2005; Gaujour et al. 2012; Plieninger 2012). Nowadays the remaining grasslands are highly fragmented, the patches are smaller and inter-patch distances longer than the previous situation and many studies have indicated a substantial loss of former species diversity (Strijker 2005; Krauss et al. 2010; Hooftman and Bullock 2012; Wallin and Svensson 2012). As a result, the remaining semi-natural grasslands are threatened and a substantial part of their species pool is considered prone to extinct (Raunio et al. 2008; Rassi et al. 2010). In addition to the specialized plant species of these habitats, the consequences of fragmentation have been equally detrimental to all the organisms that depend on them (Arlt et al. 2008; Taboada et al. 2011; Littlewood et al. 2012; Griffith et al. 2012).

It is evident that the important ecological values of semi-natural grassland have become threatened as the quantity and quality of semi-natural grassland has declined, thus breaking a long historical habitat continuum. At the same time as agricultural practices have become more homogenized and common agricultural policy is focusing on competitiveness and productivity (Walters et al. 2012), however, the significance of agricultural diversity in semi-natural grasslands has been increasingly recognized. They are challenging management and conservation targets but restoration actions have been introduced in many parts of Europe to bring back some of these habitats and strengthen the connectivity between the existing fragments. The European Union has also been eager to offer support for grazing and management of semi-natural grasslands through environmental protection schemes, targeted at continuing, or in some cases reintroducing, past management practices (Luoto et al. 2003; Kuussaari et al. 2008). Restoration of the former semi-natural grasslands is the main tool to increase the habitat

area, relying mostly on plants that have survived in a seed bank or refuge habitats, or are being spontaneously dispersed from nearby populations (Helm et al. 2006; Kuussaari et al 2009; Dahlström et al. 2010; Auffret and Cousins 2011a). If the habitat degradation has not continued for too long and there are other viable populations in the vicinity, these methods are justified.

For successful restoration, understanding the preconditions that have created and maintained diverse semi-natural grasslands is essential, both for finding the most prominent restoration targets and for developing an optimal strategy for their further management. Long-term, continuous grazing and/or mowing and lack of fertilization on open or partly open grasslands are recognized as essential preconditions to inhibit a build-up of soil nutrients and prevent fast growing, competitive species to achieve dominance (Kull and Zobel 1991; Eriksson et al. 1995; Cousins and Eriksson 2002; Schaffers 2002; Price 2003). In a fragmented landscape, rotating grazing cattle between grasslands can also facilitate seed dispersal and make them less prone to species loss (Auffret et al. 2012). Partial scrub or tree coverage on semi-natural grasslands has also been found to have positive effects on plant species as well as on other taxa (Pykälä 2000a; Söderström et al. 2001; Pihlgren and Lennartsson 2008; Gazol et al 2012). Heterogeneous grazing, mowing and clearing regimes with varying intensities can be used to support seed dispersal and regeneration of specialized grassland plants, offer suitable habitats for a number of insect species as well as provide a safe nesting period for birds (Söderström et al 2001; Steward and Pullin 2008; Reitalu et al. 2012). To maximize the benefits of grassland management, practical planning solutions have focused on the spatial and temporal optimization of grazing and/or mowing, to sustain a sufficient amount of semi-natural grassland habitats of various characteristics (Vessby et al. 2002; van Teeffelen et al. 2008; Öckinger et al. 2012).

Restoration, however, requires both time and resources to bring back the previous habitat conditions to be managed again, and its success is far from guaranteed. Patches of previous semi-natural grassland are likely to contain seeds of previous vegetation in the soil but this seed bank may not be viable anymore after a long period of overgrowth

(Milberg 1995; Kalamees and Zobel 1998; Pywell et al. 2002; Wagner et al. 2003). If previous grasslands have overgrown to coniferous forest, habitat quality may be lowered due to needle and litter accumulation, reduction of light availability and changes in soil chemistry (Alriksson and Olsson 1995; Janišova et al. 2007). In terms of wind-derived dispersal, the effective range of many grassland plants is less than a few meters, and is thus a serious obstacle for spontaneous regeneration (Bakker and Berendse 1999; Soons et al. 2005).

Another point of view for restoration success is provided by state-and-transition models, suggesting that even a careful repetition of all the ceased activities may not necessarily bring back the previous state. This may occur when a certain threshold is surpassed, leading the vegetation to turn from one stable state to another and virtually irreversible state (Briske et al. 2005; Bestelmeyer et al. 2009). This re-transition resilience may be caused by shifts in species dominance, trophic interactions and/or the invasion of exotic species, and the concomitant effects on biochemical processes, in addition to the ecological reasons mentioned above (Suding et al. 2004). External, uncontrolled processes, such as the fertilization effects of air-borne nitrogen, can also impair the success of restoration (Bobbink et al. 1998; Carly et al. 2010). According to some studies, nitrogen and the eutrophication of the Baltic Sea have assisted the overgrowth of vegetation and speeded up the changes in the island flora (Hannus and von Numers 2010, von Numers 2011; Bahr et al. 2012).

Although all the restoration-related factors cannot be known or anticipated, it is important to rationalize the selection of the most potential, feasible and cost-effective targets based on the conditions that can be reliably observed and estimated. Field inventory, carefully conducted by an experienced expert familiar with local conditions, is the principal tool to evaluate the present state and restoration capabilities of semi-natural grasslands. If local expertise is deficient, there is a risk that important targets may be unintentionally missed or overlooked due to the paucity of information on landscape trajectories, or if the optimal habitat patches cannot be found. In addition, if focusing on large functional habitat networks, this procedure can turn out to be slow and tedious without systematic foreknowledge of the habitat characteristics. These facts have been realized in the contemporary conservation planning but in practice, handling data on previous landscape characteristics is often inadequate. Historical sources may be used in the planning process but often in a manual way as supportive material during the fieldwork, thus lacking positional accuracy and full potentialities provided by the construction of landscape trajectories prior to fieldwork period.

To response to these needs, systematic retrospective interpretation of grassland dynamics is needed to allow for the identification of continuities and disturbance regimes over decades or even centuries. Its principal advantages are to offer improved understanding of the habitat's condition and the associated biodiversity as well as provide tools to evaluate responses for restoration actions (Käyhkö and Skånes 2008). Such systematic trajectory analysis of past land cover and land use characteristics can be performed by combining spatial data sources with a GIS software, including old aerial images, cadastral maps or written records that enable spatial and temporal interpretation of landscape dynamics (Cousins and Eriksson 2002; Käyhkö & Skånes 2006; Gustavsson et al. 2007; Dahlström et al. 2010; Reitalu et al. 2010).

In this paper we present a conceptual framework for evaluating the restoration potential of semi-natural grasslands in a moderately transformed agricultural environment, based on spatial data and exemplified through a partially overgrown and selectively managed grassland area in south-western Finland. We anticipate that a combined knowledge of the past and present grassland structures in the landscape mosaic plays a crucial role in the pre-assessment and site identification during a semi-natural grassland restoration planning. On the basis of the spatio–temporal landscape trajectory analysis, we construct potential restoration scenarios based on the expected semi-natural grassland continuum and date of overgrowth. These scenarios are evaluated using landscape metrics, their feasibility is discussed and the effects of potential restoration are compared to the present extent of open semi-natural grasslands.

Materials and methods

Study area

The framework of constructing restoration scenarios is exemplified in the Archipelago National Park, south-western Finland, where long-term traditional agriculture and moderate human influence have formed a mosaic of grasslands and forests in between the barren bedrock hills. The Archipelago National Park, presently occupying an area of about 50,000 hectares, was established in 1983 to preserve the diverse natural and cultural peculiarities of the area, which hosts the highest level of rare and threatened species of all the nature conservation areas in Finland (Metsähallitus 2000). It is certified by the PAN (Protected Area Network) Parks Foundation, set up by the WWF to safeguard European wilderness for future generations and balance protection with management actions. In addition, Archipelago National Park forms the core area of the Archipelago Sea Biosphere Reserve, established by UNESCO in 1984 to promote sustainable development and research on the interdependency between man and nature (IUCN 2013). The high occurrence of esker islands, diverse grasslands and coastal habitats have also resulted in the Archipelago Sea being recognized as one of the top priority areas in terms of landscape management (Mikkonen and Moilanen 2013). The area belongs to the hemiboreal zone, characterized by influences of a boreal climate but favorable for Pendunculate Oak (Quercus robur) and many other temperate deciduous trees. The average yearly temperature in the region is +6.1 °C, with monthly averages ranging from -1.1 °C in January to +18.6 °C in July, as recorded in the Utö meteorological station; the yearly rainfall is approximately 600 mm (Kersalo and Pirinen 2009).

The Archipelago National Park is managed by the state-owned Metsähallitus Natural Heritage Services and plays an essential role in preserving the remnants of the seminatural grasslands in the region. In the late 19th century the area was much more densely populated than it is today and virtually all the available grassland resources were used for grazing, hay making and, to a lesser extent, field cultivation (Kotiluoto 1998; Lindgren 2000). Rotation of domestic animals from one island to another was necessary to avoid overuse of the grasslands and such management regimes also helped to establish functional connections between the grassland patches (Auffret 2011b; Auffret et al. 2012). Beginning in the early 20th century, and increasing more rapidly after the mid-1900s, gradual depopulation and cessation of management started to turn the previously open grasslands into scrubland and forest vegetation. Recently, some of the overgrown areas have been restored by Metsähallitus and present management actions for selected grassland areas include pollarding, mowing and grazing. These activities have contributed to the survival of semi-natural grassland species and strengthened the functionality of the grassland ecosystems but may not be enough to ensure the long-term persistence of populations. As further restoration would still be needed but resources to perform it are scarce, there is a need to find the most potential and cost-effective targets.

To demonstrate the trajectory approach in finding the most prominent targets and estimation of grassland restoration potential, we selected the Berghamn hamlet with its three largest islands — Berghamn (63 ha), Mälhamn (36 ha) and Boskär (78 ha) — as our case study area (Fig. 1). These islands are all characterized by barren bedrock hills, rising up to 40m above sea level and occupying approximately 40 % of the land area, while the remaining areas have provided scarce grassland resources, albeit sufficient to feed the cattle, sheep and goats (Mussaari et al. 2012). The main island of Berghamn has been permanently inhabited for centuries, while the uninhabited islands of Mälhamn and Boskär have been mainly used as additional grazing grounds. At the beginning of the 20th century there were still high numbers of cattle and sheep kept on grasslands, commonly owned by the hamlet (Mussaari et al. 2012). Some of the lush grasslands were fertilized by cattle manure, and made more productive through the establishment of drainage systems. Field cultivation was practiced on small and temporary plots, however. Similarly to the surrounding region, the cessation of management resulted in overgrowth from the early 1900s, first affecting the outlying Boskär and Mälhamn — as their resources were no longer needed — and later the village island of Berghamn. Nowadays, part of the overgrown semi-natural grasslands have been restored by Metsähallitus but

the remaining areas are variously occupied by tall grasses, scrubland or forest vegetation of different ages.

Figure 1 Map of the study area (data from the National Land Survey of Finland, 2012)

Study materials and classification of single image layers

The study was based on maps and aerial images from the years 1890–2008, which formed the foundation for the detection of landscape trajectories (Fig. 2, Table 1). The oldest data source was a hand-drawn general parceling map from the year 1890, which was initially produced to divide the hamlet area, previously commonly owned by all the villagers, into privately owned plots of single farms. The land division was based on sharing a certain amount of agricultural resources for every farm; a smaller area of fertile land corresponded to a larger area of infertile land, thus making it important to evaluate the productivity rates of each land unit (Saarenheimo 1983).

Figure 2 Data sources used to define landscape trajectories: general parceling map from 1890 (National Archives of Finland); aerial image from 1939 (Finnish Defence Forces Military Intelligence Center, license 104/2010); aerial image from 1963 (National Land Survey of Finland); and aerial image from 2008 (Blom Finland).

Data source	Year	Original purpose	Information contents	Classification	Data extents	Additional rema
General parceling map, drawn by J.F. Henelius under he original name: Renovation i 3 delar af Karta bifver Berghamns bys samtliga egor	1890	Division of commonly owned land into shares of single farms	Land use map including supplemental information on land ownership and productivity; hand drawn by a surveyor at a nominal scale of 1 : 8000	Classes drawn on the map were Åker och tomter (plots of gardens, yards and small temporary fields), Äng (grasslands highly suitable for mowing or grazing) and Absolut skogsmark (mostly forests and bedrock areas but also including grasslands less suitable for mowing or grazing due to e.g. stony ground). This classification, however, was constructed to reflect generalized land use characteristics and not applicable as such to observe biotopes or habitats. Known locations of semi-natural grasslands, for example, were found both from <i>Äng</i> as well as <i>Absolut skogsmark</i> classes. Thus, interpretation of land cover characteristics was not performed for parceling map but only productivity rate was used as an indicator of the supposed management intensity.	Whole Berghamn hamlet, consisting of several separate map sheets and supplemental pages	All the figures mark on the map were numbered and supplemental information on productivity rate, a owner of the plot a further remarks we given on separate sheets. Geometricc accuracy of the ma was regarded as b good enough for th analysis.
Aerial image, produced by the Finnish corps of opographical engineers	1939	General mapping purposes, preparation of topographical maps	Raw grayscale analogous aerial image taken approximately at a nominal scale of 1 : 20000	The following classes were interpreted and delineated from all the aerial image layers, based on visual stereoscopic interpretation: (1) grassland, open or partly open (2) scrubland (3) deciduous-dominated forest (4) coniferous-dominated forest (5) other land cover types	Berghamn, Mälhamn and Boskär, covered by 8 partially overlapping image frames	Rectification was problematic due to missing orientatior parameters, qualit images was good.
Aerial image, produced by the National Land Survey of Finland	1963	General mapping purposes, preparation of topographical maps	Raw grayscale analogous aerial image taken at a nominal scale of 1 : 31000		Berghamn, Mälhamn and Boskär, covered by 5 partially overlapping image frames	Somewhat grainy images but enoug interpreting major cover characteristi
Aerial image, produced by Blom Finland	2008	General mapping purposes, vegetation mapping	Both raw and ortho-corrected colour+NIR digital aerial images acquired at a pixel ground resolution of 20 cm		Berghamn, Mälhamn and Boskär, covered by 11 partially overlapping image frames and orthomosaic	Very good-quality sharp images, NIR channel extending interpretation capabilities

Productivity of the parceling map was scaled between 0.1 and 10 and marked on supplementary sheets; however, instead of being a standard measure of absolute quality, it was defined as a relative ratio between the different polygons drawn on the same map sheet (Vitikainen 2003). Productivity rates were established in cooperation with local farmers and based on realized yields rather than absolute fertility potential, resulting in intensively managed land plots near to the village gaining generally higher values than extensively used areas farther away (Hiironen 2012). However, as parceling was used as a basis for further taxation and required approval from all the farms prior to validation, it can be regarded as a fairly reliable document of contemporary land productivity. During the field visits in 2010–2011, areas exceeding a productivity rate of 4 were observed to often have signs of previous ditches and characterized by highly level surface with homogeneous, lush vegetation. Thus, they were interpreted as areas of high productivity with vegetation composition being likely to show signs of intensive management and probable application of manure. All of these high-productive plots were either present or previous grasslands, temporary fields, gardens or yards.

The time series of aerial images used in the study consisted of three data layers, acquired in the years 1939, 1963 and 2008. The two oldest layers were scanned, analogue, grayscale spring images, enabling a general interpretation of the vegetation types, grassland characteristics and topographic variation. The latest images from the year 2008 were digital, high-accuracy midsummer images, acquired in the visible and near-infrared wavelengths. The interpretation capabilities provided by these images extended to reliable observations of fine-scale surface structures, vegetation heights and canopy details. Frequent field visits in 2010–2011 familiarized the researchers with the study area and helped to refine the classification of the remotely sensed data sets. Interpretation was further assisted by the recent topographic database of the National Land Survey of Finland.

Rectification of the 1890 map was performed against the contemporary topographic maps and orthomosaic of the year 2008, collecting a sufficient amount of dispersed control points from old buildings, sharp corners of real estate borders and unaltered, reliably

distinguishable landscape elements. This procedure was carried out using Erdas Imagine software (ERDAS 2010), rectifying the map with a second order polynomial function. The results appeared to be satisfactory after a visual analysis with most of the observed errors remaining within a few meters distance, high-productive areas generally being mapped more accurately than plots of infertile land. The use of a more complicated rectification methodology, as suggested for example by Cousins (2001), was not considered necessary. After rectification, all the polygons drawn on the map were digitized using ArcGIS 10.1 (ESRI 2012) software and their productivity rates were updated in the attribute table.

The raw aerial image frames were rectified using block triangulation by the Leica Photogrammetric Suite, part of Erdas Imagine software, and by collecting reference points from the orthomosaic of the year 2008. Digitization of land-cover classes was performed by stereoscopic interpretation, using a minimum mapping unit of 0.1 ha which was found to be the best compromise between the highly heterogeneous environment, the aims of the study and the practical efforts of classification. The procedure was performed in a retrospective order, starting from the 2008 images and then continuing back through the older images, thus allowing a reconstruction of the past by regressing from the relatively well known present (Skånes and Bunce 1997).

Five land-cover classes were separated from the aerial images: grassland, scrubland, deciduous-dominated forest, coniferous-dominated forest and other (Table 1). The grassland class included all areas likely to be dominated by grassland vegetation at the ground layer, ranging from open to partly open grasslands with partial canopy coverage or scrub vegetation. The determining factor for distinguishing grassland from scrubland or forests was the visibility of grassland vegetation between the trees or scrubs; clearly separable grassland patches were regarded as indicating at least partially non-overgrown situations and the presumable survival of significant amounts of grassland vegetation, thus classified as grassland. Patches dominated seamlessly by bushes, junipers or low trees were assigned to the scrubland class while tree-covered areas, with a continuous canopy structure, were classified as forests and further divided into deciduous- and

coniferous-dominated stands. Other land-cover types included rocky areas, characterized by a predominance of barren bedrock outcrops, and reed-growing areas affected by seawater.

Classification of change trajectories and construction of scenarios

After classifying all the separate image layers, change trajectories and management and restoration scenarios were extracted from the results. First, six different combinations of landscape continuum were recognized on the basis of overlaying all the single layers (Table 2), aiming to describe the supposed degree of deterioration of the present seminatural grassland habitat. Such trajectory analysis helps in identifying the core character of a landscape and thereby offers useful information for the practical planning of management and conservation (Käyhkö and Skånes 2006).

Table 2 Definition of landscape trajectory classes.

Trajectory class	Description			
1A	Permanently classified as grassland from 1939 to 2008, with a productivity rate of 4 or less			
18	Overgrown to forest or scrubland in 1939 and/or 1963 but detected as grassland in 2008, with a productivity rate of 4 or less			
2	Grassland in 1939 and/or 1963 but overgrown to scrubland or deciduous forest in 2008, with a productivity rate of 4 or less			
3	Grassland detected only in 1939 and classified as scrubland or deciduous forest between 1963 and 2008, with a productivity rate of 4 or less			
4A	Present or overgrown grasslands on high-productive ground, with a productivity rate of more than 4			
4B	No grassland detection from 1939 to 2008 or previous grassland overgrown to coniferous forest			

The classification was based on the permanency of grassland vegetation, the time span of detected overgrowth, productivity rates of the parceling map and detection of coniferous overgrowth. Classes 1A–B were regarded as having the strongest indication of present semi-natural grassland characteristics, with a long and uninterrupted (1A), or temporarily ceased and later restored (1B) grassland continuum on low-productive ground. Classes 2 and 3 included recently (2) or earlier (3) overgrown low-productive grasslands, providing potentialities for further restoration actions. The remaining areas were classified into classes 4A and 4B, suggesting an expected high deterioration, lack of semi-natural grassland characteristics or change into a new stable state. In class 4A, including present or overgrown grasslands on high-productive ground, this classification was based on the assumption of more intensive management, thus reducing species richness and impeding potential restoration actions (Berendse *et al.* 1992; Eriksson *et al.* 1995). The low potential of class 4B was justified by the fact that the aerial images from 1939 to 2008 had not indicated any grassland phases or that previous grasslands had overgrown to coniferous forest, markedly reducing the expected habitat conditions.

The trajectory classes were grouped together into three management and restoration scenarios, reflecting present grassland extents and restoration potential based on the supposed habitat quality (Fig. 3). Core areas were defined, including trajectories 1A-B, indicating the total current grassland area of expected semi-natural characteristics. This reflects the recommended minimum extents of present management, given that further losses are not allowed, and offers a premise to evaluate the scale and effects of the potential restoration actions of the two remaining scenarios. The extended core scenario includes, in addition to trajectories 1A-B, recently overgrown areas (trajectory class 2) that can be expected to possess a significant number of semi-natural grassland characteristics and have the highest potential for restoration. The maximum limits scenario consisted of trajectory classes 1A-B, 2 and 3, and reflects the largest potential area of semi-natural grasslands, provided that restoration is also extended to long overgrown habitats. Practical constraints and long-term habitat deterioration, however, may pose practical obstacles, especially for restoring the areas of trajectory class 3. Trajectory classes 4A and 4B are left outside of all the scenarios due to their expected poor semi-natural quality.

Figure 3 Relation of trajectory classes (1A–4B, inside solid lines) with management and restoration scenarios (inside dashed lines).

Evaluation of management and restoration scenarios based on landscape indices

Landscape configuration of management and restoration scenarios was measured using five widely applied landscape indices: total area (TA), percentage of landscape (PL), number of patches (NP), effective mesh size (EMS) and connectance index (CI). These indices were regarded as giving a good overall perception of the habitat extents and the level of fragmentation - significant for the conservation of species without being too focused for a single species or functional group. Shape-related indices were left out of the scope of this analysis due to their problematic interpretation, specificity for detailed purposes and potential shortcomings in a semi-natural environment where the shapes of patches are often elongated and the location of their borders modified by human activities (Moser et al. 2002; Haines-Young and Chopping 1996). When constructing the indices, each study island was regarded as being an independent and separate landscape element, segregated from the adjacent islands by comparatively large sea areas. Although species may in reality have functional connections over the whole study area, facilitated by external vectors such as cattle (Auffret et al. 2012; Rico et al. 2012), interaction and dispersion is highly limited between the islands, thus supporting the recognition of them as independent units. The indices were calculated using ArcGIS 10.1 (ESRI 2012) and Fragstats 4.1 (McGarigal et al. 2012) software and prior to calculation, patch fragments of less than 100 m² were removed due to their negligible effect on habitat characteristics.

Of the measured indices, TA and PL operate at the total habitat level, NP and EMS emphasize characteristics and fragmentation of habitat patches and CI measures the degree of spatial patch aggregation, altogether providing a good basis for estimating the present state and the effects of the suggested restoration scenarios. When proceeding from one scenario to another, the habitat area increases via three principal processes: expansion of existing separate patches, merging of two separate patches by amalgamation and emergence of new patches. Different metrics have different sensitivities and responses to these change processes, thus complementing each other (Table 3).

Table 3 Expected responses of landscape metrics to increasing habitat area. Responses:- = negative response, 0 = no response, + = positive response and ++ = strong positiveresponse.

¹⁾ Depends on the spatial configuration of patches and used threshold distance

	Total area / percentage of landscape	Number of patches	Effective mesh size	Connectance index ¹⁾
Expansion of the existing patches	+	0	+	++/+/0
Merging of separate patches	+	-	++	++/+/0
Emergence of new patches	+	+	+	++ / + / -

Total area indicates the combined extent of all the patches, without considering their spatial arrangement or relative abundance in the landscape. It has, however, high relevance in evaluating the costs of conservation actions and given a certain amount of resources, as there may be a maximum limit not to be exceeded. As a counterpart for total area, percentage of landscape relates the absolute habitat coverage to the surrounding matrix and provides a fractional measure of habitat dominance, also helping to compare landscapes of different extents.

Number of patches reflects the potential effects of restoration if implemented according to the scenarios, indicating whether the emergence of new patches or amalgamation of existing patches is a dominant process. NP, however, is not an adequate measure of patch dynamics and fragmentation *per se*; simultaneous emergence and amalgamation may have profound effects on the landscape configuration but in terms of NP, the two processes can overrule each other. For that reason, effective mesh size was selected to complement the evaluation, capable of reacting to a range of landscape processes that contribute to habitat fragmentation (Llausás and Nogué 2012). EMS was introduced by Jaeger (2000) and can be interpreted as an average habitat area surrounding a randomly selected location within the habitat patches (Girvetz et al. 2008). If compared to the

commonly used index of mean patch size, EMS is area-weighted, thus not similarly sensitive to the omission or inclusion of small patches, and it has been successfully applied to various studies regarding to grassland fragmentation (Mitchley and Xofis 2005; Gottschalk et al. 2007; Baldi and Paruelo 2008). Effective mesh size is measured in area units and at its maximum can gain the same value as total area, given that all the area is consisted of suitable habitat.

Furthermore, landscape fragmentation in terms of the spatial arrangement of patches was measured using the connectance index. CI is defined as the number of functional joinings between patches within a user-defined distance, reported as a percentage of the maximum possible connectance given the number of patches (McGarigal et al. 2012). Although the connectance value will be highly affected by the emergence or amalgamation of habitat patches and thus cannot on its own provide clear information about conservation value (Heleno et al. 2012), it can be a useful indicator of patch aggregation when applied in conjunction with map interpretation and other indices. As this study does not focus on any specific organism, the connectance threshold was defined based on physical landscape characteristics and CI values were interpreted as a measure to facilitate management actions, movement of cattle between the patches and dispersion of mobile species. Since the extents of typical rocky hills on the study area vary between 100 and 300 meters from edge to edge, and they can efficiently separate the low-lying areas of the opposite sides, the connectance threshold was selected to be 100 m, thus focusing on the adjacent patches that have the best capabilities for functional linkages.

Results

Detected changes on the study islands between 1939 and 2008

Of the three observed islands, Berghamn has always had the highest amount of highproductive grassland, consisting major part of the present total coverage in the study area (Fig. 4). During the study period of 1939–2008, Berghamn's high-productive grasslands have slightly declined but low-productive ones have declined even more significantly, indicating that regardless of recent restoration actions the trend has been towards the disappearance of grasslands. Due to natural succession development, these grasslands have overgrown into scrubland and deciduous forests. Coniferous trees are few in number on Berghamn and have never gained dominance while other land cover types, consisting mostly of infertile bedrock outcrops, have remained fairly unaltered.

Figure 4 Classifications of single aerial image layers 1939–2008, indicated as proportions of the separate islands and the total coverage.

Mälhamn, located approximately 750 m away from Berghamn as measured by the closest shore-to-shore distance, shares many characteristics with the village island: both high- and low-productive grasslands have occupied substantial areas, coniferous coverage has always been virtually negligible and bedrock-dominated areas have remained unchanged. Grasslands restoration, however, has been more effective, especially for the low-productive plots: a decline between 1939 and 1963 turned into an increase between 1963 and 2008, while the opposite trend can be observed for scrubland and deciduous forest. Boskär, located 1.5 km from Berghamn, is more dissimilar to the village island than is Mälhamn. High-productive grasslands have never existed there and coniferous forests have always been abundant. Regardless of some recent restoration actions, which can be seen in the statistics between 1963 and 2008, many of the grasslands have overgrown into forest compared to the situation in 1939. Slight changes

in the class of other land cover types are due to the expansion of coniferous trees towards the rocky hills.

Within the whole study area, landscape changes are noticeable but the effects of different islands partly overrule the detected magnitude. It is evident that grasslands have declined, especially the low-productive ones, while forest coverage has changed reciprocally. Overall, the coverage of scrubland vegetation has declined, affected mostly by shifts that occurred on Boskär. Changes of bedrock areas, comprising a major part of other land-cover classes, have been rather negligible.

In terms of change trajectories (Fig. 5), permanent (class 1A) and restored (1B) grasslands on Berghamn and Mälhamn are mostly concentrated on the sides of areas characterized by intensive management (4A), mainly forming narrow but rather well connected networks. Patches of intensively managed grasslands are quite low in number but occupy a substantial proportion of central, depressed parts on Berghamn and Mälhamn. Areas of overgrown grassland, resulting mainly from recent succession to scrubland or deciduous forest (class 2), appear rather frequently on Berghamn while their proportion on Mälhamn is smaller. The trajectory characteristics of Boskär differ markedly from the two other islands — intensive management is lacking and instead of having large, continuous and quite evenly shaped grassland-influenced patches as detected on Berghamn and Mälhamn, most of the present and former grassland are organized as relatively narrow strips stretching across the island. Early overgrown grasslands of class 3 cover larger areas on Boskär compared to the other islands.

Figure 5 Map representation showing the location and distribution of trajectory patches on the study area. Most of the area is characterized by fairly unfertile rocky hills (consisting majority of the class 4B), having high-productive grasslands (4A) and open or overgrown low-productive grasslands (1–3) at lower altitudes.

Evaluation of management and restoration scenarios

Patches included in the core areas scenario — that is, those assessed as having important contemporary semi-natural grassland characteristics — cover areas of around 7 ha on both Berghamn and Boskär, and a smaller area of 4.4 ha on Mälhamn (Fig. 6). In terms of landscape percentage, the differences are not that striking, and all the study islands remain between 9.4 and 12.1 %. Given that restoration actions are targeted to the areas of extended core habitats, including recently overgrown semi-natural grasslands, all the islands are able to gain new areas of semi-natural grassland but the increase on Berghamn is more substantial than that on Mälhamn and Boskär. The maximum limits scenario, extending restoration actions to semi-natural grasslands with more prolonged overgrowth, indicates evidence of further enlargement of grassland area on Boskär while the other islands remain close to the level of the previous scenario.

The number of patches has variable trends on different islands: on Berghamn, especially when comparing core and extended core scenarios, the merging of separate patches is a clearly dominant process and patch numbers are being significantly decreased. Mälhamn remains quite unaltered between the scenarios, or at least no dominating process of creating or merging of patches is noticeable, while the appearance of new patches is evident on Boskär as a result of restoration. In terms of effective mesh size, Berghamn has the smallest starting value, but the increase as a result of extended core restoration scenario is substantial. Mälhamn, again, will stay rather constant throughout the scenarios and Boskär requires restoration until maximum limits to get noticeable results. Connectance between the patches shows Mälhamn to be superior compared to the two other islands, but restoration scenarios are capable of improving the situation on both Berghamn and Boskär. On Berghamn, the increase is gradual from one scenario to another, but on Boskär connectivity temporally drops at the extended core scenario, increasing again for maximum limits.

Figure 6 Calculated indices for the different management and restoration scenarios.

Discussion

Benefits and challenges of the retrospective change trajectory analysis

A detailed change trajectory analysis can be used to provide detailed information on past qualities and consequent potentialities that cannot easily be perceived by observing only the present state. Long-term historical signals in the present landscape are often weak, but recognizing them is of vital importance for gaining in-depth understanding of seminatural grasslands and their dynamics. Knowledge of landscape trajectory is capable of indicating specific locations of in-situ grassland continuums and revealing those past land-use phases which are thought to either improve or impair the ecological quality of grasslands. This refers especially to the continuity of their openness, grazing or mowing pressure and potential effects of intensive management. In the Berghamn study area, trajectory analysis indicates a polarization of the agricultural scenery where the previous landscape, characterized by well-connected grazed grasslands and transitional components between the grasslands and forests, has turned into more separated patches of still open or restored grasslands and rather thickly overgrown forests.

Observed change trajectories reflect the spatial arrangement of land-use patterns created by the traditional village structure and pinpoint the functional differences between the three study islands. Berghamn has always been the main island of the village, having the largest resource of high-productive grasslands as well as a significant amount of lowproductive ones. Overgrowth occurred on Berghamn later than on outlying Mälhamn and Boskär, indicating a longer management continuum. The actual overgrowth observed on Mälhamn is not only affected by spontaneous development but also by recent restoration. On Boskär, regardless of restoration actions focused on a limited number of locations, overgrowth appears to be the dominant process and has already been initiated by the early decline of agricultural activities. This long management history and late overgrowth of grasslands near to villages supports the suggestion of other studies that the most valuable semi-natural grasslands may often be found in the vicinity of inhabited places

rather than places farther away from villages (Lindborg and Eriksson 2004; Reitalu et al 2010).

Change trajectory analysis, however, is having limitations which have to be understood in conjunction with the interpretation of the results. First of all, these are typically based on sequential snapshots, which lack the immediate link with the changes that occurred between the time layers (Jansen et al. 2006, Käyhkö and Skånes 2006). Thus, landscape trajectories cannot explicitly indicate the accurate moment of change but only can prove that they actually have happened within a given time frame. Another shortcoming involves data quality; historical information can prove to be deficient in terms of geometric accuracy, image resolution or thematic properties, or it cannot be reliably interpreted based on present knowledge. This especially applies to old maps, where uncertainty arises from misinterpretations of the purpose, scale and time of mapping as well as generalization techniques (Vuorela et al. 2002). In addition, transferring existing information from land use to land cover, or vice versa, or between biotope (observable biotic community) and habitat (species-related entity) characteristics, may result in unsatisfactory results. An essential matter in conducting a successful trajectory analysis is the sufficient and sophisticated understanding of the study area, including knowledge of the present characteristics, dominant processes and expected time span of the observed changes. A set of presumptions always have to be made, such as management intensity in this study, but results may be of good quality if all these decisions are justified and correctly adjusted to reflect the local conditions.

Applicable classification of change trajectories is also a demanding task as each added trajectory layer will multiply the chances of different layer combinations, thus requiring simplification if it is to be practically usable. In this study, the two most crucial factors are emphasized for their impact on habitat quality: long continuum of grassland characteristics and low effects of fertilizers (see *e.g.* Eriksson et al. 1995; Myklestad and Sætersdal 2004). It is known that our study area has never been under heavy artificial fertilization, but differences in management intensity between the grassland patches are evident, with the best available data given by the field-interpreted productivity rates. One

fact which has been assumed, but not fully supported by the study materials, is the longterm continuity of the grasslands prior to 1939, forming the basis for finding valuable and restorable semi-natural grassland habitats. It is, however, known that the population of this village has been rather stable for centuries and virtually all the applicable land has been utilized for agricultural purposes prior to the recent cessation of management, giving a solid base for this premise (Mussaari et al. 2012).

Scenario construction – a tool for better spatial planning

While the importance of change trajectory analysis and historical knowledge of agrarian landscapes is often highlighted (Eriksson et al 1995; Bruun et al. 2001; Lindborg and Eriksson 2004; Lunt and Spooner 2005; Reitalu et al 2010), far less attention has been given to the question of how to support functional habitat networks by increasing the area of high-quality semi-natural grasslands. This is, however, a crucial matter in the contemporary, highly transformed agricultural landscape which may fail to preserve the diversity of semi-natural grassland specialist species. These species still keep their stronghold within a fragmented habitat network but are vulnerable for stochastic events and threatened by extinction debt (Luoto et al. 2003; Helm et al 2006; Kuussaari et al 2009; Hannus and von Numers 2010). Preserving only the remaining fragmented habitats may eventually lead to a poor ecological outcome as current observations of species occurrences are prone to overestimating long-term species richness (Helm et al. 2006, Hanski and Ovaskainen 2002). Therefore, restoration actions may be a significant factor in preserving the semi-natural species pool but limited resources must be focused on the most potential locations.

Management and restoration scenarios sketched in this study may help to answer some crucial questions: where the most potential restoration targets should be located, how tedious their restoration is expected to be, and what the benefits would be for the landscape structure. Tools to answer these questions are provided by both map visualizations and the interpretation of indicator values. Berghamn island, for example, would appear to gain substantial benefits from the restoration of recently overgrown

grasslands which would connect much of the presently separated fragments together. With a restoration area of a few hectares, as the extended core scenario suggests, the number of patches would substantially decrease and simultaneously both effective mesh size and connectance would increase. Boskär is quite opposite to Berghamn, showing only modest effects for the extended core scenario, but much better effective mesh size and connectivity values for the maximum limits scenario. Boskär is expected to require more tedious and long-term restoration actions to be accomplished. The third island, Mälhamn, indicates no substantial changes of indices between the scenarios, and the new restoration potentialities are quite few. This can be interpreted as a result of successful restoration actions so far; further restoration could be more beneficial if focused on Berghamn or Boskär rather than Mälhamn.

The quantitative information of the scenarios is useful for decision-making regarding management and restoration, usually based on predefined resources and schedule constraints. In reality, however, certain limitations have to be understood when interpreting the results of the scenarios. First of all, potential restoration areas within the same scenario are not homogeneous. Extended core scenario, for example, includes patches that may have started to overgrow between the late 1960s and early 2000s. Given that grassland habitat characteristics and dormant seed bank will gradually deteriorate along the time, some of the earlier overgrown patches may not be easily restorable anymore compared to more recently overgrown ones. This is, however, the cost of using 'snapshot' analysis where simplicity will always affect the quality of results to some degree. Many unknown or uncontrolled factors may also have a substantial effect on the outcome of restoration, making overgrown grasslands resilient to changes as highlighted within the framework of state-and-transition models. One potential way to further determine the viability of restoration would be to combine laboratory analyses of soil fertility, acidity or seed bank to refine the scenario limits. A practical constraint in the scenario implementation, however, may be land tenure, restricting whether an optimal restoration plan can be completed in all the intended locations.

The use of landscape indices can help to interpret the landscape and facilitate the understanding of the consequences of possible changes. Indices, however, have to be interpreted with sufficient care and selected in regard to the given setting. As stated by Li and Wu (2004), the ecological relevance of landscape indices is more often presumed than established, with inadequate support of empirical evidence. They can also easily neglect the underlying processes, operate in an inappropriate scale, overlook any qualitative properties or simply just be misinterpreted by the researchers (Haines-Young and Chopping 1996; Li and Wu 2004; Girvetz et al. 2008; Dramstad 2009; Visconti and Elkin 2009). For these reasons, the indices used in this study were selected based on their expected robustness and applicability for various scales, thus rather reflecting general landscape properties than being specifically targeted at any certain organism. In addition, as no single indicator is enough for producing a detailed perception of the landscape, several indices were used as a combined set to minimize the chances of misinterpretations.

Interpretation of index values is partly based on the assumed superiority of large and continuous patches instead of small and fragmented ones, an idea which has long been subject to continuous debate (e.g. Kiviniemi and Eriksson 2002; Godefroid and Koedam 2003; Heegaard et al. 2007; Parker 2012). However, solutions are often case-sensitive and in terms of practical feasibility and promoted seed dispersal, larger patches are usually considered to be a better choice. Connectance values require special attention as the used threshold is always specific to certain organisms and not universally applicable values are available. In this study, connectance was measured based on the known physical characteristics and as such it cannot be interpreted as defining a range of a certain organism. However, it can be regarded as an additional indicator of management feasibility, and its usage in the comparison of scenarios is justified given that emphasis is also placed on the absolute coverage of patches.

Some studies have suggested that the best semi-natural grassland potentialities may be found in previous intensively managed and set-aside fields rather than long overgrown non-intensive grasslands (Stadler et al. 2007; Dahlström et al. 2010). While we do not

disagree with these findings, we emphasize the combined effects of the initial habitat state, degree of landscape transformation and characteristics of the surrounding matrix as determining factors for restoration success. If overgrowth has continued for a prolonged period of time and no recognizable remnants of semi-natural grasslands are to be found in the vicinity, a certain proportion of grassland plants may be re-introduced, with the least amount of effort, to former fields. However, in terms of species highly specialized for semi-natural environments, areas formerly under intensive management will not be suitable. Furthermore, an excess amount of nutrients in the soil may support the success of fast-growing generalists, thus posing challenges for further management. Provided that remnants of a functional semi-natural grassland network still exist and overgrowth has not demolished all the previous habitat characteristics, restoration of nonintensively managed semi-natural grasslands is to be prioritized instead of former fields.

Importance of preserving semi-natural grasslands

Species of semi-natural grasslands are threatened due to ceased traditional management, and several studies have proved the ecological and cultural significance of preserving remaining semi-natural grasslands (Vainio et al 2001; Luoto et al 2003; Cousins and Eriksson 2008). Regardless of a wide awareness of this matter, however, only a minor part of European semi-natural grasslands are currently reported as having favorable conservation status and their decline and fragmentation are extensive and increasing problems in many regions (Walters et al. 2012). These processes are exemplified in our study area which reflects the recent dominance of overgrowth, regardless of intentional management and restoration actions. Many species associated primarily with semi-natural grasslands are classified as regionally extinct, endangered or vulnerable in Finland (Rassi et al. 2010, Raunio et al. 2008) and consequently, identifying and managing the remnants of these once extensive habitats is highly important. Biodiversity preservation of these species rich grasslands has been recognized as one of the key priorities both in national and European level conservation action plans (Heikkinen 2007, European Commission 2008).

The high value of semi-natural grasslands does not reside only on the existence of the habitat or single rare species but also on their important ecological, social, and cultural services which cannot be replaced by other habitats or compensated by the market (Walters et al. 2012). Grassland are, for example, beneficial in water retention and erosion control, generating chances for ecotourism, preserving important cultural heritage and helping to create the image of a vital and dynamic landscape (Eriksson et al. 2005; Lindborg et al. 2008; Bastian 2013). A diversity of flowering plants can provide resources for pollinator insects and create economic possibilities through herbal or medicinal use, or by providing seeds of locally adapted plants (Öckinger and Smith 2007; Hopkins 2009; Bastian 2013). In addition to ground layer plants, veteran trees on the grassland offer important resources for beetles and birds (lhse and Lindahl 2000). It has also been reported that dairy and meat produced by cattle grazing on semi-natural grasslands is more healthy and of better quality than of cows from intensively managed grasslands, providing an extra asset for product marketing (Wood et al. 2007; Wyss and Collomb 2008; Niemelä and Orjala 2012). Furthermore, semi-natural grasslands are an irreplaceable part of the recent cultural heritage and surrounding landscape, often greatly valued as beautiful scenery and being part of local identity (Stenseke 2006).

We studied semi-natural grasslands in the hemiboreal zone where specialization and unique species pool makes their relative importance and conservation value high. Most of the larger grassland areas in other parts of the world are markedly differing from them in terms of environmental conditions and species composition. As better habitat connectivity increases the effective dispersal of species and creates more persistent regional populations, the ongoing fragmentation of hemiboreal semi-natural grasslands is highly detrimental (Bakker and Berendse 1999; Hanski 1999; Lindborg and Eriksson 2004; Soons et al. 2005). Nature conservation, however, has to be balanced for the needs of different functional groups and cannot be targeted solely on semi-natural grasslands. These species rich grasslands are often embedded in a heterogeneous mosaic of habitats, making species diversity at the landscape scale high for not only plants but also for other organisms (Eriksson et al. 2005). Thus, conservation efforts that range from local to regional level must consider preservation of all this diversity but recognize

functionally connected semi-natural grasslands as an essential part of the landscape composition.

Conclusions

Increasing the area of managed semi-natural grasslands should be considered as one of the priorities to reach the goals set for biodiversity preservation, both at national and international levels. Uninterrupted management of existing sites is essential to be continued but to ensure the stability of habitat network and reach the favorable conservation status, restoration actions are of equal importance.

Landscape trajectory analysis and scenario construction, in a similar manner to that presented above, can be a valuable tool for the restoration planning of semi-natural grasslands and should be considered as an essential tool in the pre-stratification of restoration potentialities. Several matters of concern are highlighted above but when the analysis is carefully performed and its practical limitations are understood, the results can prove beneficial for restoration action. It must also be remembered that a favorable landscape continuum is not a guarantee of good habitat quality but only forms a basis for its emergence. Fieldwork is always required to confirm and refine the results of trajectories and scenarios, but the preliminary outcomes of the presented analysis will help to focus these efforts.

The intention of this study is not to indicate a detailed procedure to be repeated in a stepby-step manner elsewhere. Instead, it exemplifies a framework which must be tailored to be applicable for the local conditions, characteristics of semi-natural habitats and availability of data sources. Temporal layers can cover a longer or shorter time span and their number can be higher or lower than seen here, but simplicity of analysis should be emphasized to keep it feasible. Adding more layers may give more detailed results but it also leads to an increased amount of complexity, resulting in a complicated definition of trajectories and, often, a higher degree of subjectivity. In terms of workflow, the analysis will not be invalidated by some practical limitations — if for example the ortho correction of old aerial images is not possible, they can be processed in a lighter and less accurate way and still retain a decent quality for a regional approach. Therefore, we encourage the readers to assimilate the message while taking the fine details of our case study as curiosities and make an improved version of the methodology that will be suitable for semi-natural grasslands elsewhere.

References

Alriksson A and Olsson MT (1995) Soil changes in different age classes of Norway spruce (*Picea abies* (L.) Karst.) on afforested farmland. Plant Soil 168–169:103–110. doi: 10.1007/BF00029319

Arlt D, Forslund P, Jeppson T and Pärt T (2008) Habitat-Specific Population Growth of a Farmland Bird. *PLoS One* 3:1–10. doi:10.1371/journal.pone.0003006

Auffret AG and Cousins SAO (2011a) Past and present management influences the seed bank and seed rain in a rural landscape mosaic. J Appl Ecol 48:1278–1285. doi: 10.1111/j.1365-2664.2011.02019.x

Auffret AG (2011b) Can seed dispersal by human activity play a useful role for the conservation of European grasslands? Appl Veg Sci 14:291–303. doi: 10.1111/j.1654-109X.2011.01124.x

Auffret AG, Schmucki R, Reimark J and Cousins SAO (2012) Grazing network provide useful functional connectivity for plants in fragmented systems. J Veg Sci 23:970–977. doi: 10.1111/j.1654-1103.2012.01413.x

Bahr A, Ellström M, Schnoor TK, Påhlsson L and Olsson PA (2012) Long-term changes in vegetation and soil chemistry in a calcareous and sandy semi-natural grassland. Flora 207:379–387. doi: 10.1016/j.flora.2012.03.003

Bakker JP and Berendse F (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends Ecol Evol 14: 63–68. doi: 10.1016/S0169-5347(98)01544-4

Baldi G and Paruelo JM (2008) Land-Use and Land Cover Dynamics in South American Temperate Grasslands. Ecol Soc 13: 6. Available online: http://www.ecologyandsociety.org/vol13/iss2/art6/

Bastian O (2013) The role of biodiversity in supporting ecosystem services in Natura 2000 sites. Ecol Indic 24, 12–22. doi: 10.1016/j.ecolind.2012.05.016

Berendse F, Oomes MJM, Altena HJ and Elberse WTh (1992) Experiments on the restoration of speciesrich meadows in The Netherlands. Biol Conserv 62:59–65. doi: 10.1016/0006-3207(92)91152-I

Bestelmeyer BT, Tugel AJ, Peacock GL Jr., Robinett DG, Shaver PL, Brown JR, Herrick JE, Sanchez H and Havstad KM (2009) State-and-Transition Models for Heterogeneous Landscapes: A Strategy for Development and Application. Rangeland Ecol Manage 62:1–15. doi: 10.2111/08-146

Bobbink R, Hornung M and Roelofs JGM (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J Ecol 86:717–738. doi: 10.1046/j.1365-2745.1998.8650717.x

Briske DD, Fuhlendorf SD and Smeins FE (2005) State-and-Transition Models, Thresholds, and Rangeland Health: A Synthesis of Ecological Concepts and Perspectives. Rangeland Ecol Manage 58:1–10. doi: 10.2111/1551-5028(2005)58<1:SMTARH>2.0.CO;2

Bruun HH, Fritzbøger B, Rindel PO and Hansen UL (2001) Plant species richness in grasslands: the relative importance of contemporary environment and land-use history since the Iron Age. Ecography 24:569–578. doi: 10.1111/j.1600-0587.2001.tb00491.x

Carly JS, Duprè C, Dorland E, Gaudnik C, Gowing DJG, Bleeker A, Diekmann M, Alard D, Bobbink R, Fowler D, Corcket E, Mountford JO, Vandvik V, Aarrestad PA, Muller S and Dise NB (2010) Nitrogen deposition threatens species richness of grasslands across Europe. Environ Pollut 158:2940–2945. doi: 10.1016/j.envpol.2010.06.006

Cousins SAO (2001) Analysis of land-cover transitions based on the 17th and 18th century cadastral maps and aerial photographs. Landsc Ecol 16:41–54. doi: 10.1023/A:1008108704358

Cousins SAO and Eriksson O (2002) The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. Landsc Ecol 17:517–529. doi: 10.1023/A:1021400513256

Cousins SAO and Eriksson O (2008) After the hotspots are gone: Land use history and grassland plant species diversity in a strongly transformed agricultural landscape. Appl Veg Sci 11:365–374. doi: 10.3170/2008-7-18480

Dahlström A, Rydin H and Borgegård S-O (2010) Remnant habitats for grassland species in an abandoned Swedish agricultural landscape. Appl Veg Sci 13:305–314. doi: 10.1111/j.1654-109X.2009.01068.x

Dramstad WE (2009) Spatial metrics – useful indicators for society or mainly fun tools for landscape ecologists? Nor Geogr Tidskr 63:246–254. doi: 10.1080/00291950903368359

ERDAS (2010) ERDAS Field Guide. ERDAS Inc., Norcross, Georgia.

Eriksson Å, Eriksson O and Berglund H (1995) Species abundance patterns in Swedish semi-natural pastures. Ecography 18:310–317. doi: 10.1111/j.1600-0587.1995.tb00133.x

Eriksson O, Cousins SAO and Bruun HH (2002). Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. J Veget Sci 13: 743–748. doi: 10.1111/j.1654-1103.2002.tb02102.x

Eriksson O, Cousins SAO and Lindborg R (2005). Land use history and the build-up and decline of species richness in Scandinavian semi-natural grasslands. In: Milne JA (ed) Pastoral systems in marginal environments. Wageningen Academic Publishers, Wageningen, pp. 51–60.

ESRI (2012). ArcGIS 10.1 SP1 for Desktop. Redlands, California

European Commission (2008) The European Union's Biodiversity Action Plan. Halting the loss of biodiversity by 2010 – and beyond. Office for Official Publications of the European Communities, Luxembourg.

Gaujour E, Amiaud B, Mignolet C and Plantureux S (2012) Factors and processes affecting plant biodiversity in permanent grasslands. A review. Agron Sustain Dev 32:133–160. doi: 10.1007/s13593-011-0015-3

Gazol A, Tamme R, Takkis K, Kasari L, Saar L, Helm A and Pärtel M (2012) Landscape- and small-scale determinants of grassland species diversity: direct and indirect influences. Ecography 35:944–951. doi: 10.1111/j.1600-0587.2012.07627.x

Girvetz EH, Thorne JH, Berry AM and Jaeger JAG (2008) Integration of landscape fragmentation analysis into regional planning: A statewide multi-scale case study from California, USA. Landsc Urban Plan 86:205–218. doi: 10.1016/j.landurbplan.2008.02.007

Godefroid S and Koedam N (2003) How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? Glob Ecol Biogeogr 12:287–298. doi: 10.1046/j.1466-822X.2003.00035.x

Gottschalk TK, Diekötter T, Ekschmitt K, Weinmann B, Kuhlmann F, Purtauf T, Dauber J and Wolters V (2007) Impact of agricultural subsidies on biodiversity at the landscape level. Landsc Ecol 22: 643–656. doi: 10.1007/s10980-006-9060-8

Griffith GW, Roderick K, Graham A and Causton DR (2012) Sward management influences fruiting of grassland basidiomycete fungi. Biol Conserv 145:234–240. doi: 10.1016/j.biocon.2011.11.010

Gustavsson E, LennartssonT and Emanuelsson M (2007) Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biol Conserv 138:47–59. doi: 10.1016/j.biocon.2007.04.004

Haines-Young R and Chopping M (1996) Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. Progr Phys Geogr 20: 418–445. doi: 10.1177/030913339602000403

Hannus J-J and von Numers M (2010) Temporal changes in the island flora at different scales in the archipelago of SW Finland. Appl Veg Sci 13:531–545. doi: 10.1111/j.1654-109X.2010.01092.x

Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford.

Hanski I and Ovaskainen O (2002) Extinction Debt at Extinction Threshold. Conserv Biol 16:666–673. doi: 10.1046/j.1523-1739.2002.00342.x

Heegaard E, Økland RH, Bratli H, Dramstad WE, Engan G, Pedersen O and Solstad H (2007) Regularity of species richness relationships to patch size and shape. Ecography 30:589–597. doi: 10.1111/j.0906-7590.2007.04989.x

Heikkinen I (ed) (2007) Luonnon puolesta – ihmisen hyväksi. Suomen luonnon monimuotoisuuden suojelun ja kestävän käytön strategia ja toimintaohjelma 2006–2016. Finnish Ministry of Environment, Helsinki.

Heleno R, Devoto M and Pocock M (2012) Connectance of species interaction networks and conservation value: Is it any good to be well connected? Ecol Indic 14: 7–10. doi: 10.1016/j.ecolind.2011.06.032

Helm A, Hanski I and Pärtel M (2006) Slow response of plant species richness to habitat loss and fragmentation. Ecol Lett 9:72–77. doi: 10.1111/j.1461-0248.2005.00841.x

Hiironen J (2012) Peltotilusjärjestelyn vaikutuksista ja kannattavuudesta. Dissertation, Aalto University.

Hooftman DAP and Bullock JM (2012) Mapping to inform conservation: A case study of changes in seminatural habitats and their connectivity over 70 years. Biol Conserv 145:30–38. doi: 10.1016/j.biocon.2011.09.015

Hopkins A (2009). Relevance and functionality of semi-natural grassland in Europe – status quo and future prospective. International workshop of the SALVERE-Project. Agricultural Research and Education Centre, Raumberg-Gumpenstein.

Ihse M (1995) Swedish agricultural landscapes – patterns and changes during the last 50 years, studied by aerial photos. Landsc Urban Plan 31:21–37. doi: 10.1016/0169-2046(94)01033-5

Ihse M, Lindahl C (2000) A holistic model for landscape ecology in practice: the Swedish survey and management of ancient meadows and pastures. Landsc Urban Plan 50:59–84. doi: 10.1016/S0169-2046(00)00080-3

IUCN (2013) Where wilderness meets the Baltic Sea. http://www.iucn.org/knowledge/focus/previous_focus_topics/marine_2010/marine_protected_areas/?524 4/Where-wilderness-meets-the-Baltic-Sea. Accessed 19 August 2013.

Jaeger JAG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landsc Ecol 15:115–130. doi: 10.1023/A:1008129329289

Janišova M, Hrivnák R, Gömöry D, Ujházy K, Valachovič M, Gömöryová E, Hegedüšová K and Škodová I (2007) Changes in understorey vegetation after Norway spruce colonization of an abandoned grassland. Ann Bot Fenn 44:256–266.

Jansen LJM, Carrai G, Morandini L, Cerutti PO and Spisni A (2006) Analysis of the spatio-temporal and semantic aspect of land-cover/use change dynamics 1991-2001 in Albania at national and district levels. Environ Monit Assess 119:107–136. doi: 10.1007/s10661-005-9013-8

Kalamees R and Zobel M (1998) Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, western Estonia. Acta Oecologia 19:175–180. doi: 10.1016/S1146-609X(98)80021-0

Käyhkö N and Skånes H (2006) Change trajectories and key biotopes – Assessing landscape dynamics and sustainability. Landsc Urban Plan 75:300–321. doi: 10.1016/j.landurbplan.2005.02.011

Käyhkö N and Skånes H (2008) Retrospective land cover/land use change trajectories as drivers behind the local distribution and abundance patterns of oaks in south-western Finland. Landsc Urban Plan 88:12–22. doi: 10.1016/j.landurbplan.2008.07.003

Kersalo J and Pirinen P (eds) (2009) Suomen maakuntien ilmasto. Raportteja 2009:8. Finnish Meteorological Institute, Helsinki.

Kiviniemi K and Eriksson O (2002) Size-related deterioration of semi-natural grassland fragments in Sweden. Divers Distrib 8:21–29. doi: 10.1046/j.1366-9516.2001.00125.x

Kotiluoto R (1998) Vegetation changes in restored semi-natural meadows in the Turku archipelago, SW Finland. Plant Ecol 136:53–67. doi: 10.1023/A:1009781217847

Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, Kuussaari M, Lindborg R, Öckinger E, Pärtel M, Pino J, Pöyry J, Raatikainen KM, Sang A, Stefanescu C, Teder T, Zobel M and Steffan-Dewenter I (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol Lett 13:597–605. doi: 10.1111/j.1461-0248.2010.01457.x

Kull K and Zobel M (1991) High species richness in an Estonian wooded meadow. J Veg Sci 2:715–718. doi: 10.2307/3236182

Kuussaari M, Heliölä J, Tiainen J and Helenius J (eds) (2008) Maatalouden ympäristötuen merkitys luonnon monimuotoisuudelle ja maisemalle. Finnish Environment Institute, Ministry of Agriculture and Forestry and Ministry of Environment, Helsinki.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M and Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. Trends Ecol Evol 24:564–571. doi: 10.1016/j.tree.2009.04.011

Li H and Wu J (2004) Use and misuse of landscape indices. Landsc Ecol 19, 389–399. doi: 10.1023/B:LAND.0000030441.15628.d6

Lindborg R and Eriksson O (2004) Historical landscape connectivity affects present plant species richness. Ecology 85:1840–1845. doi: 10.1890/04-0367

Lindborg R, Bengtsson J, Berg Å, Cousins SAO, Eriksson O, Gustafsson T, Hasund KP, Lenoir L, Pihlgren A, Sjödin E and Stenseke M (2008) A landscape perspective on conservation of semi-natural grasslands. Agric Ecosystems Environ 125: 213–222. doi: 10.1016/j.agee.2008.01.006

Lindgren L (2000) Island pastures. Edita, Helsinki.

Littlewood NA, Steward AJA and Woodcock BA (2012) Science into practice – how can fundamental science contribute to better management of grasslands for invertebrates? Insect Conserv Divers 5:1–8. doi: 10.1111/j.1752-4598.2011.00174.x

Llausàs A and Nogué J (2012) Indicators of landscape fragmentation: The case for combining ecological indices and the perceptive approach. Ecol Indic 15:85–91. doi: 10.1016/j.ecolind.2011.08.016

Lunt ID and Spooner PG (2005) Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. J Biogeogr 32:1859–1873. doi: 10.1111/j.1365-2699.2005.01296.x

Luoto M, Rekolainen S, Aakkula J and Pykälä J (2003) Loss of Plant Species Richness and Habitat Connectivity in Grassland Associated with Agricultural Change in Finland. Ambio 32:447–452. doi: 10.1579/0044-7447-32.7.447

McGarigal K, Cushman SA and Ene E (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available online: http://www.umass.edu/landeco/research/fragstats/fragstats.html

Metsähallitus (2000) Saaristomeren kansallispuiston runkosuunnitelma. Edita, Helsinki.

Mikkonen N and Moilanen A (2013) Identification of top priority areas and management landscapes from a national Natura 2000 network. Environ Sci Policy 27:11–20. doi: 10.1016/j.envsci.2012.10.022

Milberg P (1995) Soil seed bank after eighteen years of succession from grassland to forest. OIKOS 72:3–13. doi: 10.2307/3546031

Mitchley J and Xofis P (2005) Landscape structure and management regime as indicators of calcareous grassland habitat condition and species diversity. J Nat Conserv 13: 171–183. doi: 10.1016/j.jnc.2004.12.001

Moser D, Zechmeister HG, Plutzar C, Sauberer N, Wrbka T and Grabherr G (2002) Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. Landsc Ecol 17: 657–669. doi: 10.1023/A:1021513729205

Mussaari M, Käyhkö N, Haggrén G, Jansson H, Lindgren L, Pitkänen T and Raatikainen K (2012) Management guidelines for semi-natural landscapes – Integrating historical perspectives and GIS into planning process. NATURESHIP publications. Metsähallitus and University of Turku, Turku.

Myklestad Å and Sætersdal M (2004) The importance of traditional meadow management techniques for conservation of vascular plant species richness in Norway. Biol Conserv 118:133–139. doi: 10.1016/j.biocon.2003.07.016

Niemelä M and Orjala M (2012) Eläimet rantaan – kyllä vai ei? Opas kestävään rantalaiduntamiseen. NATURESHIP publications. MTT Agrifood Research Finland and Centre for Economic Development, Transport and the Environment (CEDTE) for South-west Finland

von Numers M (2011) Sea Shore Plants of the SW Archipelago of Finland – Distribution Patterns and Long-Term Changes during the 20th Century. Ann Bot Fenn 48:1–46. doi: 10.5735/085.048.SA01

Öckinger E and Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. J Appl Ecol 44:50–59. doi: 10.1111/j.1365-2664.2006.01250.x

Öckinger E, Lindborg R, Sjödin NE and Bommarco R (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. Ecography 35:259–267. doi: 10.1111/j.1600-0587.2011.06870.x

Parker S (2012) Small Reserves Can Successfully Preserve Rare Plants Despite Management Challenges. Nat Areas J 32:403–411. doi: 10.3375/043.032.0409

Pärtel M, Bruun HH and Sammul M (2005) Biodiversity in temperate European grasslands: origin and conservation. In: Lillak R, Viiralt R, Linke A and Geherman V (eds) Integrating Efficient Grassland Farming and Biodiversity. Proceedings of the 13th International Occasional Symposion of the European Grassland Federation, Tartu, Estonia, 29–31 August 2005, pp. 1–14.

Pihlgren A and Lennartsson T (2008) Shrub effects on herbs and grasses in semi-natural grasslands: positive, negative or neutral relationships? Grass Forage Sci 63, 9–21. doi: 10.1111/j.1365-2494.2007.00610.x

Plieninger T (2012) Monitoring directions and rates of change in trees outside forests through multitemporal analysis of map sequences. Appl Geogr 32:566–576. doi: 10.1016/j.apgeog.2011.06.015

Price EAC (2003) Lowland Grassland and Heathland Habitats. Routledge, London.

Pykälä J (2000a) Traditional rural biotopes in Finland. In: Ikonen I and Lammi A (ed) Traditional rural biotopes in the Nordic countries, the Baltic states and the Republic of Karelia. Nordic Council of Ministers, Copenhagen, pp 14–21

Pykälä J (2000b) Mitigating Human Effects on European Biodiversity through Traditional Animal Husbandry. Conserv Biol 14:705–712. doi: 10.1046/j.1523-1739.2000.99119.x

Pywell RF, Bullock JM, Hopkins A, Walker KJ, Sparks TH, Burke MJW and Peel S (2002) Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. J Appl Ecol 39:294–309. doi: 10.1046/j.1365-2664.2002.00718.x

Rassi P, Hyvärinen E, Juslén A and Mannerkoski I (ed) (2010) The 2010 Red List of Finnish Species. Ministry of Environment and Finnish Environment Institute, Helsinki.

Raunio A, Schulman A and Kontula T (eds) (2008) Suomen luontotyyppien uhanalaisuus – Osa 1. Tulokset ja arvioinnin perusteet. Finnish Environment Institute, Helsinki.

Reitalu T, Johansson LJ, Sykes MT, Hall K and Prentice HC (2010) History matters: village distances, grazing and grassland species diversity. J Appl Ecol 47:1216–1224. doi: 10.1111/j.1365-2664.2010.01875.x

Reitalu T, Purschke O, Johansson LJ, Hall K, Sykes MT and Prentice HC (2012) Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialization. J Veg Sci 23:41–51. doi: 10.1111/j.1654-1103.2011.01334.x

Rico Y, Boehmer HJ and Wagner HH (2012) Determinants of actual functional connectivity for calcareous grassland communities linked by rotational sheep grazing. Landsc Ecol 27: 199–209. doi: 0.1007/s10980-011-9648-5

Robertson JGM, Eknert B and Ihse M (1990) Habitat Analysis from Infra-Red Aerial Photographs and the Conservation of Birds in Swedish Agricultural Landscapes. Ambio 19:195–203.

Saarenheimo J (1983) Isojaot ja isojaonjärjestelyt. In: Maanmittaus Suomessa 1633–1983. Maanmittaushallitus, Helsinki, pp 20–62.

Schaffers AP (2002) Soil, biomass and management of semi-natural vegetation – Part II. Factors controlling species diversity. Plant Ecol 158:247–268. doi: 10.1023/A:1015545821845

Skånes HM and Bunce RGH (1997) Directions of landscape change (1741–1993) in Virestad, Sweden – characterised by multivariate analysis. Landsc Urban Plan 38:61–75. doi: 10.1016/S0169-2046(97)00019-4

Slotte H (2001) Harvesting of leaf-hay shaped the Swedish landscape. Landsc Ecol 16:691–702. doi: 10.1023/A:1014486331464

Söderström B, Svensson B, Vessby K and Glimskär A (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodivers Conserv 10:1839–1863. doi: 10.1023/A:1013153427422

Soons MB, Messelink JH, Jongejans E and Heil GW (2005) Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. J Ecol 93: 1214–1225. doi: 10.1111/j.1365-2745.2005.01064.x

Stadler J, Trefflich A, Brandl R and Klotz S (2007) Spontaneous regeneration of dry grasslands on setaside fields. Biodivers Conserv 16:621–630. doi: 10.1007/s10531-005-0604-z

Stenseke M (2006) Biodiversity and the local context: linking seminatural grasslands and their future use to social aspects. Env Sci Policy 9: 350–359. doi: 10.1016/j.envsci.2006.01.007

Stewart GB and Pullin AS (2008) The relative importance of grazing stock type and grazing intensity for conservation of mesotrophic 'old meadow' pasture. J Nat Conserv 16:175–185. doi: 10.1016/j.baae.2005.01.00110.1016/j.jnc.2008.09.005

Strijker D (2005) Marginal lands in Europe – causes of decline. Basic Appl Ecol 6:99–106. doi: 10.1016/j.baae.2005.01.001

Suding KN, Gross KL and Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. Trends Ecol Evol 19: 46–53. doi:10.1016/j.tree.2003.10.005

Svenning J-C (2002) A review of natural vegetation openness in north-western Europe. Biol Conserv 104: 133–148. doi: 10.1016/S0006-3207(01)00162-8

Taboada A, Kotze DJ, Salgado JM and Tárrega R (2011) The value of semi-natural grasslands for the conservation of carabid beetles in long-term managed forested landscapes. J Insect Conserv 15:573–590. doi: 10.1007/s10841-010-9359-2

van Teeffelen AJA, Cabeza M, Pöyry J, Raatikainen K and Kuussaari M (2008) Maximising conservation benefit for grassland species with contrasting management requirements. J Appl Ecol 45:1401–1409. doi: 10.1111/j.1365-2664.2008.01514.x

Vainio M, Kekäläinen H, Alanen A and Pykälä J (2001) Suomen perinnebiotoopit. Perinnemaisemaprojektin valtakunnallinen loppuraportti. Finnish Environment Institute, Helsinki.

Vessby K, Söderström B, Glimskär A and Svensson B (2002) Species-Richness Correlations of Six Different Taxa in Swedish Seminatural Grasslands. Conserv Biol 16:430–439. doi: 10.1046/j.1523-1739.2002.00198.x

Visconti P and Elkin C (2009) Using connectivity metrics in conservation planning – when does habitat quality matter? Diversity Distrib 15, 602–612. doi: 10.1111/j.1472-4642.2009.00564

Vitikainen A (2003) Uusjakojen toimitusmenettelyn uudistamisesta. Dissertation, Helsinki University of Technology.

Vuorela N, Alho P and Kalliola R (2002) Systematic Assessment of Maps as Source Information in Landscape-change Research. Landsc Res 27:141–166. doi: 10.1080/01426390220128631

Wagner M, Poschlod P and Setchfield RP (2003) Soil seed bank in managed and abandoned seminatural meadows in Soomaa National Park, Estonia. Ann Bot Fenn 40:87–100.

Wallin L and Svensson BM (2012) Reinforced Traditional Management is Needed to Save a Declining Meadow Species. A Demographic Analysis. Folia Geobot 47:231–247. doi: 10.1007/s12224-012-9123-3

Walters LJ, Lindhagen A, Delbaere B, Arvela M, Hyvärinen E, Lammerant J, Leivits A, Loosveldt K and Urtans A (2012) Boreal Natura 2000 Seminar Report. European Center for Nature Conservation, Tilburg.

Whitehouse NJ and Smith DN (2004) 'Islands' in Holocene forests: Implications for Forest Openness, Landscape Clearance and 'Culture-Steppe' Species. Environ Archaeol 9: 203–212. doi: 10.1179/146141004790734397

Wood JD, Richardson RI, Scollan ND, Hopkins A, Dunn R, Buller H and Whittington FM (2007) Quality meat from biodiverse grassland. In: Hopkins JJ, Duncan AJ, McCracken DI, Peel S and Tallowin JRB (eds) High value grassland: providing biodiversity, a clean environment and premium products. Proceedings of the BGS/BES/BSAS Conference held at Keele University, Staffordshire, UK, 17-19 April, 2007. pp. 107-116

Wyss U and Collomb M (2008) Influence of forage from grassland on the fatty acid content of milk fat. In: Hopkins A, Gustafsson T, Bertilsson J, Dalin G, Nilsdotter-Linde N and Spörndly E (eds) Biodiversity and animal feed: future challenges for grassland production. Proceedings of the 22nd General Meeting of the European Grassland Federation, Uppsala, Sweden, 9-12 June 2008. pp. 421-423

Figure 1 (fitted for 129 mm width) Click here to download Figure: Fig1_129mm.eps



Figure 2 (fitted for 129 mm width) Click here to download Figure: Fig2_129mm.eps





Figure 3 (fitted for 84 mm width) Click here to download Figure: Fig3_84mm.eps

1939

1963









Figure 6 (fitted for 129 mm width) Click here to download Figure: Fig6_129mm.eps



Acknowledgements

This study was financially supported by the NATURESHIP project (EU Central Baltic Interreg IV A), the Maj and Tor Nessling Foundation and the University of Turku, Department of Geography and Geology. We also thank the anonymous reviewers and the Editorial Board for their useful and constructive comments, helping us to make important improvements for the manuscript.