How has time and space affected plant biodiversity in the Hjälmö-Lådna archipelago?

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Cover pictures

left: a detail from the cadastral map of Gällnö village from 1640; middle: Raymond Ringqvist moves live-stock to Hjälmö Västerholme (photo: J. Reimark); right: an aerial view of the Hjälmö-Lådna archipelago from the north (photo: S. Cousins)
Abstract

Traditionally European farmland management has declined during the last century, mainly due to abandonment or intensification. When traditional management is replaced by new methods many species are negatively affected and often threatened with extinction. In this thesis, the Stockholm archipelago is used as a platform to study the effects of land use change over time. The overall aim is to examine how time and space affects plant biodiversity in a rural landscape, with focus on heterogeneous pastures.

Historical records and maps were interpreted together with aerial photos and used to construct four time-layers of land use: reflecting the landscape 200 years ago, 100 years ago, 50 years ago and present. Investigations of plant species richness was conducted in seven habitats; 1) grazed fields, 2) grazed forest edges, 3) grazed forest interior, 4) former grazed fields, 5) former grazed forest edges, 6) former grazed forest interior, and 7) historical pasture islands, on 35 islands in Hjälmö-Lådna archipelago on the east-coast of Sweden. Plant species richness was measured for all plant species and for grassland specialist species at three scales: i) fine-scale diversity ($\alpha_{\text{div}}$), ii) large-scale diversity ($\gamma_{\text{div}}$), and iii) spatial turnover ($\beta_{\text{div}}$). Using Structural Equation Models (SEM) the variation in species diversity and plant community composition was investigated in relation to landscape context, space and management history.

The land use change in the Hjälmö-Lådna archipelago followed the general trends on the mainland in Sweden and the rest of Europe with loss of traditional managed habitats, such as meadows or wooded pastures. However, no intensification and large-scale agriculture has developed on the islands, mainly because of physical limitations, but also because of economical and conservation reasons. Surprisingly, the grazing pressure on the remaining grazed habitats had not changed notable over the last century; although the study area was not particularly species rich (highest average was 15 species/ m$^2$ in grazed fields). Adjacent habitats; field and wood pasture, showed a higher similarity in community composition than expected compared to random pairs. Grazing and proportion of openness had a positive influence on species richness and especially on grassland specialists. The variation of total diversity at the landscape scale was best explained by the heterogeneity of grazed forest edges and the local species diversity in fields.

The results from the study suggest that grazing is important also in species-poor landscapes, and that it can aid in protecting and promote species-richness also in other types of species-poor landscapes. To prevent further loss of biodiversity it is necessary to keep fields and forest edges open with continuous management. To maintain values of high biodiversity and culture in the archipelago it is therefore important that farmers are subsidised by EU to continue to graze heterogeneous habitats and pastures with many trees.
List of papers

I. Reimark, J., Schmucki, R., Cousins, S.A.O,
200 years of grassland management and the relationship to present plant species richness in a rural archipelago landscape in the Baltic Sea. Manuscript to be submitted to Applied Vegetation Science after revision

II. Schmucki, R., Reimark, J., Lindborg, R., Cousins, S.A.O,
How does variation in landscape context and management history structure plant diversity in grassland communities? Submitted manuscript

Author’s contribution to the papers:

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Introduction

Land use change is currently the main global driver of biodiversity loss (Sala et al., 2000). In Europe, farm abandonment or intensification of farm land are current threats to biodiversity, as traditional management is replaced by new methods that affect many species negatively. The Stockholm archipelago provides an excellent platform to study the effects of land use change over time on plant species diversity and composition at different scales. Here, we find a remnant rural landscape with a mosaic of forest and small fields. In the Swedish archipelago as well as in the rest of Europe, farmers have a long tradition of using heterogeneous wooded pastures (Vera 2000, Gimmi et al. 2008). These wooded pastures were utilized in several aspects; grazing, fuel and timber, by pollarding and shredding of trees for fodder. All together this created semi-open to open heterogeneous grassland habitats. Many wooded pastures in Europe were abandoned in the beginning of the 20th century as more intense cattle farming and forestry developed. In Sweden livestock grazed the forests until regulations protecting the forest industry’s interests were proclaimed in the 1920s. However, in remote and less productive areas the tradition was carried on until the 1950s (Dahlström 2008). The contemporary pasture structure in the archipelago is reminiscent of the historical wooded pastures; here they graze whole islands, including shores, forests and former arable fields.

There are few remnants of grazed forest left in Europe, and they are now targets for biodiversity conservation (EEA 2010a, b). The Swedish Environmental Quality Objective nr 10 (Swedish Ministry of the Environment 2005), which states “Coasts and archipelagos must be characterized by a high degree of biological diversity and a wealth of recreational, natural and cultural assets.” highlights the importance of management strategies that promote biodiversity in the archipelago. EUs current regulations on the maximum tree density, 60 trees per hectare in pastures, make it difficult for farmers in Sweden to keep heterogeneous pastures (Swedish Ministry of Agriculture 2010) as Swedish pastures traditionally have a high tree cover A probable consequence of these management control measures is that the few remaining wooded pastures will be abandoned in the future and important cultural and natural values will be lost (Bergmeier et al. 2010).

Grazing affects plant species richness depending on the grazing intensity; extensive grazing and long continuity is shown to promote high plant species diversity (Bruun et al. 2001; Evans et al. 2006; Gustavsson et al. 2007; Pavlu et al. 2007; Dumont et al. 2009; Reitalu et al. 2010). Dahlström (2008) developed the concept grazing equivalents, used to compare grazing intensity when live-stock animals change over time. Grazing does not only affect plant species richness but also species composition (Diaz et al 2007; Dumont et al 2009). Grazing management in the archipelago requires moving livestock by boat between islands from May to October depending on quality of the pasture (Hedenstierna 1949). This forms a network of islands visited by the same livestock over the grazing season. A more recent element in the agricultural landscape...
in general is grazed former arable fields. Studies show that these field can contribute positively to plant species diversity and affect community composition in a landscape context (Cousins and Aggemyr 2008, Brückman et al. 2010, Auffret 2011). Most studies that examined the effect of landscape context on plant diversity focus on single rather than multiple habitat types, when using a patch-based approach. Yet, accumulating evidence shows that grassland plant species can inhabit various habitats and not only open grazed habitats (Cousins and Eriksson 2001, Dahlström et al. 2010). By disregarding the effect of adjacent habitats, a single habitat approach cannot adequately address the complexity of the processes controlling diversity patterns in complex landscapes.

When trying to estimate species diversity in complex landscapes it is important to measure at different scales (Cousins and Vanhoenacker 2011). Species diversity can be measured as the local diversity within a patch, i.e. alpha diversity ($\alpha_{div}$), and beta diversity ($\beta_{div}$), i.e. the diversity between patches. Both diversity values contribute to the gamma diversity ($\gamma_{div}$) (Whittaker 1972), which can be considered as an estimation of heterogeneity in species diversity (Hendrickx et al. 2007). Especially species affiliated to certain habitats; so called specialist species, and particularly those associated with habitats common in the historical landscape are affected when the land use change (Lindborg and Eriksson 2004; Milden et al. 2007; Bergmeier et al. 2010). The subgroup of grassland plant specialists, defined as plant species promoted by management (grazing or mowing) (Ekstam and Forshed 1992; Lindborg 2007; Krauss et al. 2010), is therefore often used as indicator of habitat quality. On the other hand, other species benefit from land use changes. Thus a mere count of species can seldom reflect the effect on plant communities when species turnover can change the composition without affecting the species number.
Objectives

The overall aim with this licentiate thesis is to explore how time and space affect biodiversity in a rural landscape. While many studies have investigated the effects on diversity caused by loss of open semi-natural grasslands, (Adriaens et al. 2006; Cousins et al. 2007; Krauss et al. 2010) I have focused on the loss of heterogeneous pastures and the effect on plant species diversity. More specific research questions were; 1) How have land use and land cover in the Stockholm archipelago changed during the last 200 years?, 2) How are plant species richness and community composition in pastures affected by these changes?, 3) In what way can heterogeneous pastures contribute to plant diversity? The licentiate thesis is a compiled thesis containing a summary of the most important results from two papers, and the two papers (hereafter called Paper I and Paper II). This thesis does not cover the history of the archipelago in other aspects than farming and grazing, although other aspects, like, fishing and hunting might be important. Moreover, how plant diversity is affected by long-term changes like climate change is not investigated.

Figure 1. An aerial view of the Hjälmö-Lådna archipelago east of Stockholm (Sweden) in the Baltic Sea. The large island in the foreground is Lådna. (Photo: S.A.O. Cousins 2010)
Methods

Study area

The Stockholm archipelago on the east coast of Sweden in the Baltic Sea consists of approximately 24000 islands, ranging from small skerries to large islands with permanent residents. The selected study area; the Hjälmö-Lådna archipelago, covers 60 km² (midpoint 59° 25' N, 18° 42' E, Fig 2) and consists of 103 islands ranging from 0.26 ha to 526 ha. The Hjälmö-Lådna archipelago has fairly dry summers and relatively mild winters. Mean annual temperature is 6.4 °C (-3.1°C January, 16.7 °C July) and mean annual precipitation is 500 mm (Alexandersson and Eggertsson Karlström 2001).

Figure 2. The Hjälmö-Lådna archipelago is located on the east coast of Sweden in the Baltic Sea. Black islands, a total of 103 islands and skerries, denote the study area.

The scattered islands with thin soil-layers (mostly moraines) (Svedmark 1883) are greatly influenced by the isostatic uplift since the end of the last glaciation, 10 000 years ago. The potential in the archipelago for intensive farming is restricted by the landscapes’ physical properties, where soils that are possible to cultivate are very limited. The landscape is similar to the rural landscape typical in Sweden from early 1900s to 1950s. The larger islands have had permanent settlements by farmers at least since 16th century (Hedenstierna 1949), but the population has never been dense. In the archipelago each farm usually had a number of smaller islands of various sizes used for grazing and hay-collecting. On islands where soils were deep enough the farmers also had crop-production. Since 1980, more than 50% of the study area is managed as nature
reserve by the Archipelago Foundation in Stockholm County with the objective to protect biodiversity and the historical archipelago farming system, including traditional grazing management.

**Land use change data**

Sweden has a unique archive of large-scale maps, usually 1:4000, covering enclosed land (i.e. infields) around villages or hamlets with detailed information on land-cover and land use, as well as written records on yields (Cousins 2009). The historical records from the study area date as far back as the thirteenth’s century (Quist 1949), but cadastral maps which reflect land use were first produced in seventeen’s century. Unfortunately these early maps did not cover all islands in the area, but written records held information about the usage of the islands not included in the maps, for example pasture or hay-collecting. Later maps, from the eighteen’s century, included all islands. Cadastral maps from three time-periods; 1741 - 1859, 1901-1906 and 1952 together with aerial photos from 1958 and 2005 were used to analyze the land use change over a period of 200 years (Fig 3). In total, four GIS layers were created, depicting the landscape 200 years ago (17/1800s), 100 years ago (1900s), 60 years ago (1950s) and

![Figure 3. The rural landscape around Gällnö village in a) 1741, b) 1906, c) 1958 (cadastral maps) and d) 2005 (IR aerial photo). In the 1741 map (a) green areas denote meadows and pink areas denote arable fields. In 1906 (b) the meadows have been transformed to arable fields (dark pink). The arable fields in 1958 (c) (yellow) and in 2005 (d) (light blue) have almost the same distribution. It is visible that the large expansion of arable fields and transformation of meadows took place before 1906. In 2005 (d) some of the former arable fields are summer house properties.](image-url)
present day (2000s). The maps were rectified, interpreted and digitised in the geographical information system (GIS) ArcGis 9.2. The aerial photographs were interpreted in the software Erdas Imagine 9.2 (Leica Geosystems Geospatial Imaging 2008) with Stereo Analyst and the land covers were digitised into the GIS. Land use was classified in two steps; a general level classifying openness of the forest canopy cover and a more detailed level classifying land-cover and land use. Land use change was calculated in ArcGis 9.2 with Overlay technique (Union tool).

To be able to analyse changes in numbers of farms and grazing intensity, historical records regarding farms practices from 1910 (Stockholms läns hushållningssällskap 1910) and 1949 (Värmdö Kristidsnämnd 1949) were analyzed together with information from local farmers. To compare grazing pressure over time the concept grazing equivalents according to Dahlström (2008) were used. This is particularly useful when more than one kind of livestock is grazing the pastures. Dahlström (2008) based the conversions of livestock numbers to grazing equivalents on fodder requirements for different animals, thus one cow is equivalent to 1.0 grazing equivalent (geq); one sheep to 0.21 geq and one horse to 1.4 geq. We used grazing equivalents measured per hectare grazed land (geq/ha) as an estimate of grazing intensity (Paper I).

**Habitat and plant species data**

Seven different habitats, reflecting typical land cover changes, were selected from the GIS land-cover layers from early 1900s, mid 1950s and early 2000s in addition with records of grazing management during the last 100 years (paper I). The habitats were: 1) grazed fields, 2) grazed forest edges, 3) grazed forest interior, 4) former grazed fields, 5) former grazed forest edges, 6) former grazed forest interior, and 7) historical pasture islands. All selected fields were used for crop-production in the early 1900s. Wooded pasture habitats were forest edges around fields, forest interior and historical pasture islands. For the second study (Paper II) 25 non-overlapping landscapes, hereafter called sites, were selected from the early 2000s GIS. The sites had a 500 m radius with a field and an adjacent wood pasture in its centre. For each site, the proportion open habitat in 1950 and 2004 was calculated. The field investigation was carried out in 2009 during six weeks from June to August on 35 islands; encompassing three farm islands and 32 satellite islands. Ten 1 m × 1 m sample plots were evenly distributed over each habitat per island and all species in each plot was recorded. Total species richness (local species pool) per habitat was measured by walking in an even stride over the whole habitat.
Figur 4. Four of the seven classes of habitats; A) grazed field; B) former grazed field; C) grazed forest interior; D) historical pasture island, used in paper I.

Analyses

From the field investigation a subset of 61 species, typical for Swedish grassland habitats, were selected based on a database of grassland specialist species in Europe (Krauss et al. 2010). Three measures of diversity (Paper I) were computed for each of the seven habitats for total plant richness and for grassland specialists: i) fine-scale diversity ($\alpha_{\text{div}}$), ii) large-scale diversity ($\gamma_{\text{div}}$), and iii) spatial turnover ($\beta_{\text{div}}$). For Paper II herbaceous species, know to be used to enhance fodder quality in cultivated fields in the archipelago (i.e. Phleum pratense, Festuca pratensis, Lolium perenne, Trifolium pratense, and Plantago lanceolata), and tree species were excluded from further analyses. In Paper II we wanted to test for difference in species diversity and composition similarity between adjacent field and wood pasture, and therefore we conducted pair wise $t$-tests at two scales: 1) average species density per 1-m$^2$ and 2) total diversity per habitat. This analysis was computed both for all plant species and for the subset containing only grassland specialists. In Paper II a structural equation modelling (SEM) was developed to investigate the direct and indirect effects of variations in landscape context, spatial distance, and management history, on species diversity and composition. All statistical analyses were computed with the open source software package R 2.11.1 (R Development Core Team. 2010) and the appropriate additional package Nonparametric Multiple Comparisons (npmc) (Munzel 2008).
Results

Land use change

The land use changes over the last 200 years in the rural landscape of the Hjälmö-Lådna archipelago are in line with general trends in Sweden, as well as in Europe (Paper I). The most significant change in land cover occurred between 1900s and 1950s, when semi-open forests became increasingly dense. Today, there is 1% of semi-open forest left, whereas 100 years ago more than 70% of the landscape was classified as semi-open forest. 200 years ago 10% of the area was meadow, but at the beginning of the 20th century most meadows had been transformed into arable fields. The extent of arable fields was highest 100 years ago, representing 11% of total land area, followed by a decline to 6% in the present landscape. The abandonment of arable fields started in 1900s, but fields were continuously kept open which is visible in the class former arable field, both in 1950s and 2000s (Fig. 5). Houses and gardens have increased from less than 1% in 1900s to 8% today, but are probably underestimated, as houses are not always visible on aerial photographs and “gardens” in the archipelago are seldom well defined. Evidence of long continuity with farming practices on the islands is shown by the fact that three farms have been situated on the same place since the 17th century (Källman 1991), and the fourth farm since 1836. An inventory of households in 1910

![Flow chart showing the major transitions (in hectares) of the six major land use/land covers classes from 17/1800 to 2000s in the Hjälmö-Lådna archipelago farming system on the east coast of Sweden. The boxes are in proportion to area (ha).](image-url)
listed 25 farmers in the study area, 50 years later there were 16, and today four farmers are left. 40% of the total land area is grazed today, compared with over 80% in 1950s and earlier. However, the proportions between grazed open fields and forests have not changed much. The increase in live-stock number from 249 in 1910 to 313 in 2009 is a consequence of a change in animal farming from dairy to meat production and where sheep is more common in the study area today. Somewhat surprisingly, the grazing pressure today is the highest during the last century, with 0.14 – 0.26 geq/ha today compared to 0.05 – 0.14 geq/ha in 1950s and 0.10 – 0.14 geq/ha in 1900s (Table 1).

Interestingly, the land still used by farmers resembles the historical rural landscape, with small and scattered fields and live-stock moving freely over larger areas containing both open fields and forests.

Table 1. The proportion of grazed land, grazing pressure measured as grazing equivalents (geq/ha) and number of farms from 1900s to 2000s in the Hjälmö-Lådna archipelago on the east coast of Sweden. Live-stock data is from historical records and information from the farmers.

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<td>73</td>
<td>39</td>
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<tr>
<td>(open/closed)</td>
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<td>(13/87)</td>
<td>(15/85)</td>
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<tr>
<td>Grazing pressure (geq/ha)</td>
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<td>0.09</td>
<td>0.17</td>
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<td>4</td>
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<tr>
<td>Live-stock (total)</td>
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<td>126</td>
<td>313</td>
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<tr>
<td>Horses</td>
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<tr>
<td>Cattle</td>
<td>120</td>
<td>103</td>
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<tr>
<td>Sheep</td>
<td>100</td>
<td>0</td>
<td>231</td>
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Plant species richness

A total of 353 different plant species were found in the survey. The most species-rich habitat was grazed field, both when all vascular plant species (15/m²) or the sub-selection grassland specialist species (7/m²) were analysed (Paper I). Historical pasture islands were poorest in species at all spatial scales. The largest difference in species richness, between open field and wooded pasture, was found for the sub-selection of grassland specialists in grazed habitats, for both fine-scale diversity ($\alpha_{div}$) and large-scale diversity ($\gamma_{div}$). Grazing had a diversifying effect on species richness as the grazed habitats were significantly different from each other where former grazed habitats were not. Spatial turnover ($\beta_{div}$) was highest in grazed forest edges and grazed or former grazed forest interior for all species. Field habitats (grazed and former grazed fields) had low spatial turnover ($\beta_{div}$) for both all species and the sub-selection grassland species (Paper I).
Figure 6. Two examples of pasture islands that belong to farms on Gällnö (cadastral map from 1741); Lammskär and Gyltholmen. Both islands were grazed in 1950, but are now abandoned. On Lammskär 37 plant species, whereof six were grassland specialist species were found, and on Gyltholmen 42 plant species, whereof seven were grassland specialist species.

In the study using 25 sites (Paper II) a total of 199 plant species were found, including 40 grassland specialists. We counted an average of 12.4 and 11 species per m² in field and wood pasture, respectively. Field habitat had a significantly higher $\alpha$-diversity than adjacent wood pasture, but this did not translate to $\gamma$-diversity, i.e. the total diversity of the habitat. When testing for similarities in plant community composition between habitats we found the highest similarity between habitats with similar conditions; field versus field and wooded pasture versus wooded pasture. However, adjacent habitats with contrasting conditions, field versus wooded pasture, showed a higher similarity than random pairs. We observed similar patterns for both scales; all species and grassland specialists, except that similarity values for grassland specialist species showed less variation among strata, and that the values computed between wood pastures was not significantly different from similarities observed between adjacent habitats with contrasting conditions (Fig. 7).
Figure 7. Average similarity (vertical dashed line) between pairs of plan communities sampled in field and adjacent wood pasture computed for (a) all species and (b) grassland specialists. Field-wood pasture (dashed line), field-field (solid line), and wood pasture-wood pasture (dash-dotted line)(Paper II).

Structured equation models (SEM) at both habitat and landscape scale are presented in paper II. The results showed that at habitat scale the SEM indicate that variation in $\gamma$-diversity was best explained by $\beta$-diversity in wood pastures and by $\alpha$-diversity in field habitats. In other words, the total diversity in a landscape was explained by the heterogeneity of wood pastures and the local diversity in fields. The composition of the plant community was positively related to landscape context (proportion of open land and grazing intensity) with a higher proportion of grassland specialists when the landscape had a higher proportion of open land. Time since ploughing explained community composition in fields, but not in wood pastures. Also at landscape scale $\gamma$-diversity was positively related to landscape context, both for the whole plant community as well as the subgroup grassland specialists (Paper II).
**Discussion**

**200 years of landscape change**

In this thesis I have used historical maps and records together with plant species data, from a rural landscape in the Stockholm archipelago, to delineate 200-years of land use change and the effects on plant species diversity in different habitats. The land use in the rural landscape in the archipelago has undergone changes during the last two hundred years, following the same trend as elsewhere in Europe, with loss of traditional managed landscape elements such as meadows or wooded pastures. However, much of the present structure resembles the traditional landscape 100 years ago, as livestock today still graze a multitude of environments; open fields, forest edges, forests, shores and are not restricted to the fenced-in field pastures common in mainland Sweden. The forest has become denser, more land has been built upon and meadows have become rare. In the beginning of 1900 the trade with firewood from islands in the archipelago was a significant source of income (Quist, 1949), which most likely lead up to partially open forests. In addition the custom to cut shrubs and branches to get winter fodder also kept the forests open. Photographs from at least two of the islands 100 years ago (Quist 1949) and descriptions in literature (Hedenstierna 1949) show the islands as fairly open compared to the present (Fig 8).

![Figure 8. A view over Lådna Island around 1880. (Photo: P.L. Quist)](image)

Crop production has ceased completely on the larger satellite islands, but grazing management has kept the former cultivated fields open to a great extent. On the abandoned islands succession has led to overgrown fields or a compact and thick grass sward. The number of farms has declined dramatically during the last 100 years, and today the grassland management is a result of conservation action rather than to produce food. At present four farmers, besides grazing the islands where the farms are situated, continue to use 10 satellite islands as pastures. There was a shift in the decades before 1950s from a landscape managed for crops and grazing to a landscape characterized by numerous leisure homes.
Species richness

The currently grazed habitats in the study area; former arable fields and wooded pastures, are not very species-rich compared to similar habitats on the mainland. The most species-rich habitat is grazed former arable fields with an average of 15 plant species/m². Even fewer species were found in the grazed wooded pastures (grazed forest edges 12/m², grazed forest interior 10/m²). This was rather unexpected as these have been grazed for 200 years and have not been fertilised with artificial fertilisers, i.e. similar to semi-natural grasslands or forest edges on mainland. These numbers are low compared to species richness found in semi-natural grasslands in other studies; for example 40- 60/m² (Kull and Zobel 1991; Klimeš et al. 2001; Pykälä 2005). There are several plausible explanations to this relative low species richness. First, the landscape is young, and second, farming in the archipelago is relative recent. The first farms were established only 400 years ago, compared to the mainland where records of management imply more than 1000 years of grassland management (Widgren 1983; Eriksson et al. 2002). Many typical grassland plants are dispersal limited (Ozinga et al. 2009) and as it is an archipelago the dispersal is likely to be even more restricted, compared to the mainland. Considering this scenario, the species-richness of the former arable fields cannot be considered particularly low. Many of them have been ploughed during the last 50 years and therefore a continuous increase of species with time (Cousins and Lindborg 2008) can be expected, as long as they are kept open with grazing. Former arable fields in the archipelago are still important habitats to maintain the diversity of the landscape as long as there is enough livestock for grazing and dispersing seeds (Auffret 2011).

That extensive grazing might enhance the diversification of the landscape has been indicated in other studies, for example Kumm (2003, 2004) established this relationship in large rangelands encompassing a mosaic of semi-natural grasslands, deciduous forest, ex-arable fields and other small grassland remnants. Furthermore, grazers aid dispersal of species between habitats and thereby increase colonisation and diversity (cf. Auffret 2011; Auffret et al. submitted ms). Here, grazing had a diversifying effect on species richness as plant species communities became more homogeneous and diversity declined when grazing ceased, which confirms result from previous studies (Cousins 2009; Krauss et al. 2010). Spatial turnover ($\beta_{div}$) for all species was highest in grazed forest edges and grazed or former grazed forest interior; one explanation could be that grazing and movement of grazers between the habitats adds grassland species to interior forest habitats. The environment is also more heterogeneous in grazed forests habitats with a higher degree of local variation in for example soil-types, wetness and interaction with shrubs and tree-species. Not surprisingly, more grassland specialists were found in open habitats than in forested habitats, and most important were grazed fields with a mean of seven grassland specialists per m². This implies that keeping the fields grazed is important especially for the sub-group grassland species. Plant species generally found in grassland communities, including grassland specialists, can thrive in both grazed fields and wood pastures. Effect of adjacent habitats on species diversity has also been documented in grazed former arable field surrounded by commercial forest plantations (Cousins and Aggemyr 2008) or close to semi-natural grasslands (Öster et
Landscape context and management history showed an overarching effect on both diversity and composition of grassland species assemblage. While habitat conditions constrain species distribution, the results indicate that grassland communities are substantially influenced by the composition of species assembly in adjacent habitats. This is particularly relevant for species with traits providing them the capacity to colonize and inhabit multiple habitat types. Hence, studying dispersal ability in relation to functional traits could be an additional way to investigate the influence of the grazing networks on the plant species diversity and composition.

Grazing pressure and future grassland management for high biodiversity
Despite that more than 50% of the land used for grassland management in the study area has been lost during the last 50 years the grazing pressure on the remaining managed land is similar to previous. Extensive grazing has been shown to be positive for plant species diversity (Bruun et al. 2001; Evans et al. 2006; Gustavsson et al. 2007; Pavlu et al. 2007; Dumont et al. 2009; Reitalu et al. 2010) and the results can verify this also for a fairly species poor rural landscape. More live-stock would be preferable so that more islands and more forested habitats could be grazed, but at present the limitation lies within the manure handling (local farmer; personal communication) as there is not enough arable land available to spread the manure produced during winter. This is a practical dilemma that needs to be solved. Another conservation measure would be to carefully open up parts of the denser grazed forest by selectively cutting down trees and thereby improve the habitat for species demanding more light. The study system, as well as the Swedish archipelago in general, has been designated as important for cultural heritage and for biodiversity. In the study area the remaining structure is still in many ways resembling the historical landscape, but nevertheless it will probably change in the near future if not measures are taken to financially support the still active farmers.

Conclusions
This thesis concludes that low intensity grazing can contribute to biodiversity at several scales; within communities and between habitats, also in species-poor landscapes. Moreover, extensive grazing in heterogeneous landscapes increases plant species diversity while ceased grassland management is negative for plant richness. Most conservation and restoration efforts have so far focused on species-rich grasslands at a local scale. However, it is important to compare different landscapes to understand the underlying processes influencing species richness in anthropogenic systems, not only diversity “hot-spots”. I show that grazing is important also in species-poor landscapes. Hence, these results can be an aid in protecting species-richness also in other landscapes. To prevent further loss of biodiversity it is important to keep fields and but also forest edges open. Therefore it is important that also farmers with livestock grazing in heterogeneous habitats are subsides by EU. In order to fulfil the goals in the 10th Environmental Objective in Sweden, for example “The natural beauty, natural and cultural heritage assets, biodiversity and variation of the coastal and archipelago landscape will be maintained by prudent use.” it is crucial to maintain farmers and livestock in the archipelago.
Acknowledgements
First of all I want to thank my supervisor Sara Cousins for her inspiration and never ending patience. Thanks also to my co-supervisor Regina Lindborg for her help with the manuscripts and the much appreciated and needed pep-talks. I also want to thank my field assistants; Ida Brännäng and Björn Ringselle for their good work, and a special thanks to Kåre Bremer who generously took his time to help us out with tricky species. I feel an enormous gratitude towards all my colleagues at INK, and most of all to the members of the LEG group, without your support I would never have been able to finalise this thesis. And, of course, I would like to thank the farmers on Gällnö, Gällnönäs, Lådna and Hjälmö who generously took their time and let me see glimpses of farming in the archipelago.

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Winter in the Stockholm archipelago, Gällnö.
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200 years of grassland management and the relationship to present plant species richness in a rural archipelago landscape in the Baltic Sea

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Abstract

Question: How has past land use, especially grazing, and land use changes influenced plant species diversity in a landscape with a complex grazing system?

Location: Hjälmö-Lådna archipelago consisting of a landscape with 103 islands with a total area of 60 km² (59° 25’ N, 18° 42’ E) on the east coast of Sweden, Europe.

Methods: A GIS-model was constructed from four time-layers of landscape data based on historical maps, from more than 200 years ago and 100 years ago, and aerial photographs from the 1950s and today. Land use change and grazing pressure were analysed. Present plant species diversity was investigated at three different scales (alpha, beta, gamma) in seven habitats on 35 islands.

Results: Land use changes follow similar trajectories as in more forested landscapes on the mainland and in the rest of Europe. The numbers of farms have declined during the last 100 years, from 25 farms to four today. Grassland area has decreased with more than 50%, where small islands were abandoned first. Livestock is still moved between islands by boat creating a complex grazing system. Grazed open former arable fields and forest edges have the highest fine-scale ($\alpha_{\text{div}}$) diversity and grazing is important for plant species richness at coarser scales too. Grazing pressure is higher today but less land is grazed.

Conclusions: Also in a landscape designated to be maintained as a traditional rural landscape past land-cover changes have been substantial, threatening plant species richness today. Grazing is important for plant species diversity at all diversity scales in a species-poor landscape. To be able to maintain grassland associated species, and to prevent further loss of biodiversity it is important to keep fields and forest edges open with grazing livestock. Farmers need to be able to graze pastures with tree densities above EU regulations to maintain the typical grassland ecosystem of the archipelago.

Keywords: alpha, beta, biodiversity, gamma, grazing, historical ecology, Hjälmö-Lådna, land use, maps, traditional, Sweden, wooded pastures
Introduction

It is a well established fact that biodiversity is decreasing when traditionally managed rural landscapes are transformed, either by intensification of agriculture, or by abandonment (Cousins & Eriksson 2002; Hodgson et al. 2005; Gustavsson et al. 2007; EEA 2010a; Krauss et al. 2010). Traditionally managed rural landscapes are part of a cultural heritage and are formed by centuries of human activities (Antrop 2005), as well as by climate and physical properties, but today the remaining areas in Western Europe are few and highly fragmented (Fischer & Stöcklin 1997; Fahrig 2001; Eriksson et al. 2002). Semi-natural grasslands (unfertilized meadows and pastures) are some of the most species-rich habitats in Europe, where a long continuity of management by mowing or grazing, without applications of artificial fertilisers, have created habitats with over 40, and sometimes more than 60 plant species per square metre (Kull & Zobel 1991; Klimeš et al. 2001; Pykälä 2005). Semi-natural grasslands and wooded pastures were common habitats in the traditional rural landscape, and many studies have investigated the effects on diversity caused by loss of open semi-natural grasslands, (Adriaens et al. 2006; Cousins et al. 2007; Krauss et al. 2010) but few have focused on the loss of heterogeneous wooded pastures (but see Bergmeier et al. 2010; Garbarino et al. 2011).

Heterogeneous wooded pastures with a combination of open fields and forested areas have, in Europe, a long tradition of management (Vera 2000; Gimmi et al. 2008). These wooded pastures were utilized for livestock grazing, for fuel and timber, and also for fodder, by pollarding and shredding of trees, thus creating semi-open to open heterogeneous grassland habitat. The wooded pastures in Europe were abandoned in the beginning of the 20th century as more intense cattle farming and forestry developed. In Sweden livestock grazed forests until regulations protecting the forest industry’s interests were proclaimed in the 1920s, but in remote and less productive areas the tradition was kept for a longer time (Dahlström 2008).
Only a few remnants of grazed forest remain today, and they are now targets for biodiversity conservation in Europe (EEA 2010a; EEA 2010b). In Sweden, grazed semi-natural grasslands can have a fairly high tree density compared to open grassland in the rest of Europe (Swedish Ministry of Agriculture Swedish Ministry of Agriculture. 2010) and can even resemble a sparse forest. By including borders to other habitats and more wooded areas the heterogeneity of the landscape is increased which is shown to increase biodiversity (Kotiluoto 1998; Öster et al. 2007; Cousins & Lindborg 2008). Also other species benefit from a more heterogenic structure of the grasslands or semi-open forests such as lichens, birds, and butterflies (Söderström et al. 2001; Bergman et al. 2008; Jönsson et al. 2011). However, lately EUs regulations on the maximum tree density in pastures make it difficult for farmers to keep heterogeneous wooded pastures (Swedish Ministry of Agriculture Swedish Ministry of Agriculture. 2010). A probable consequence of these management control measures is that the few remaining wooded pastures will be abandoned in the future and important cultural and natural values will be lost (Bergmeier et al. 2010).

Species diversity in an agricultural landscape can be divided into the local diversity within a community, i.e. alpha diversity ($\alpha_{div}$), and beta diversity ($\beta_{div}$), i.e. the diversity between communities. Both diversity values contribute to the gamma diversity ($\gamma_{div}$) (Whittaker 1972), which can be considered as an estimation of heterogeneity in species diversity (Hendrickx et al. 2007). Despite being recognised as a fundamental part of spatial biodiversity patterns the division of alpha, beta and gamma diversity is a measure that is seldom used in broad-scale investigations of species richness patterns (but see Koleff et al. 2003; Crist & Veech 2006; Chiarucci et al. 2008; Rundlöf et al. 2008).

An example of a remnant rural landscape is the archipelago in the Baltic Sea, which has elements of agriculture interspersed on the islands. The land cover on larger islands is usually a mosaic of forest and small fields similar to the rural landscape typical in Sweden.
from 1900s to 1950s. The contemporary pasture structure in the archipelago is reminiscent of historical wooded pastures, where livestock was allowed to graze over larger heterogeneous areas; here they graze whole islands, including shores, forests and former arable fields. Two aspects of grazing management are of interest for this study; grazing pressure and continuity. Low-intensity grazing and long continuity is shown to promote high species diversity (Bruun et al. 2001; Gustavsson et al. 2007; Pavlu et al. 2007; Reitalu et al. 2010). However, more studies are required to understand how much and for how long grazing is needed to preserve high biodiversity. Grazing not only affects plant species richness but also species composition (Schmucki et al. submitted ms). A subgroup of so called grassland specialists, defined as plant species promoted by management (grazing or mowing) (Ekstam & Forshed 1992; Lindborg 2007; Krauss et al. 2010), is often used as indicator of habitat quality. Here we use the Hjälmö-Lådna archipelago in the Baltic Sea to investigate 200 years of land use change and the relationship to present plant species richness in a rural landscape.

The overall aim is to explore how land use over time, especially grazing, affects richness today and the possible effects in the future. We focus on heterogeneous pastures in a rural landscape that has been pinpointed as being particularly important for the cultural and biological heritage by the Swedish Government in 2005 (Swedish Ministry of the Environment 2005). Specifically, we ask (i) do land use and land-cover changes in the study area follow the same pattern as mainland Europe, (ii) how do continuity in grassland management and grazing pressure effect on plant species diversity, and finally (iii) how important are wooded pastures for plant species diversity.
Method

Study area

The study area, Hjälmö-Lådna archipelago, is approximately 60 km² and situated in the Stockholm archipelago in the Baltic Sea (midpoint 59° 25' 5.66" N, 18° 42' 16.70" E, Fig 1). Parts of the study area are a nature reserve, managed by the Archipelago Foundation in Stockholm County. The total study area consists of 103 islands with a size ranging from 0.26 ha to 526 ha (Fig 1). Dominating bedrock are granites and soil-types are moraines with elements of loamy-silt (Geological Survey of Sweden; SGU 1881). Mean annual temperature is 6.4 °C (min -3.1°C January, max 16.7 °C July) and mean annual precipitation is 500 mm (Alexandersson & Eggertsson Karlström 2001). The archipelago in the Baltic Sea is a result of isostatic uplift of land that was suppressed by the ice-sheet during the last glaciation that...
ended 10 000 years ago. When the ice retreated land began to rise again and in the study area land is still rising at a present rate of 4 mm / year. The archipelago is therefore a landscape in constant change where new islands appear and smaller islands merge together and with time form larger landmasses. As land rises above sea level the islands are subjected to wave and wind action that reallocates soil to lower ground and leave the surrounding hilltops bare of soil. Forests are dominated by Scots pine (*Pinus sylvestris*) and oak (*Quercus robus*) on thinner dry soils and Norway spruce (*Picea abies*), birch (*Betula pendula*), ash (*Fraxinus excelsior*) and willow (*Salix sp.*) on deeper and moister soils. Evidence of long continuity with farming practices on the islands is shown by the fact that three farms have been situated on the same place since the 17th century (Källman 1991) and the fourth farm since 1836.

The archipelago offers a very special and often harsh environment for farming, which has resulted in a typical archipelago farming system. The potential in the archipelago for intensive farming is restricted by the landscapes’ physical properties, were soils that can be cultivated are limited. Similar landscapes can be found on the mainland in the border landscapes between open farmland and forested areas. Larger islands in the Stockholm archipelago have had permanent settlements by farmers at least since 16th century (Hedenstierna 1949), and since the 17th century the population increased, but has during the last hundred years declined. A typical farm, 200 years ago, had a ratio of 20-30% crop fields to 70-80% meadow within the infield system (enclosed to keep livestock out) to be able to sustain livestock over the winter and at the same to get enough manure to fertilize the crop-fields (Cousins 2009). The livestock moved freely over larger areas and grazed both forest and pastures outside the infield system. In the archipelago each farm usually had a number of smaller island of various sizes used for grazing and crop-production where there were enough deep soils to cultivate. Many of these islands are still grazed today. These grazed islands,
without farms, are hereafter called satellite islands. In historical maps and written records from the 17th and 18th century it is possible to detect even smaller islands, without open fields, used for grazing only. These are hereafter called historical pasture islands (islands that have not been grazed for at least 70 years). Grazing management in the archipelago requires moving livestock by boat between islands from May to October depending on quality of the pasture (Hedenstierna 1949). Today, livestock is used for grazing management and to produce meat, but in the past milkmaids had to row out twice a day to different islands to milk the livestock.

Landscape data

To investigate land use changes cadastral maps from 18th, 19th and 20th century were used. Sweden has a unique archive of large-scale maps, usually 1:4000, covering enclosed land (i.e. infields) around villages, or hamlets, with detailed information on land-cover and land use, as well as written records on yields (Cousins 2009). The maps were rectified, interpreted and digitised in the geographical information system (GIS) ArcGis 9.2. Land use data for 1950s and 2000s were gained from interpretations of aerial photographs (black and white from 1958 and colour infra-red from 2005). Land use was classified in two steps; a general level classifying openness of the forest canopy cover and a more detailed level classifying land-cover and land use. In total, four land-cover layers were created, reflecting the landscape 200 years ago (17/1800), 100 years ago (1900s), 60 years ago (1950s) and present day (2000s). Land use change was calculated in ArcGis 9.2 with Overlay technique (Union tool). Historical records regarding livestock (horses, sheep and cows) numbers from 1910 (Stockholms läns Stockholms läns hushållningssällskap 1910) and 1949 (Värmdö Värmdö Kristidsnämnd 1949), were analyzed together with information from local farmers. To compare grazing pressure over time irrespective of kind of farm animal, the concept “grazing equivalents” according to Dahlström (2008) was used. This concept is useful when
more than one kind of live-stock is combined in pastures. We used grazing equivalents measured per hectare grazed land (geq/ha).

Species data

Seven different habitats, reflecting typical land cover changes and grazing history, was selected from GIS land-cover layers from 1900s, 1950s and 2000s, in addition to records of grazing management during the last 100 years. The habitats were 1) grazed fields, 2) grazed forest edges, 3) grazed forest interior, 4) former grazed fields, 5) former grazed forest edges, 6) former grazed forest interior, and 7) historical pasture islands. All fields were used for crop-production in the beginning of the 1900s. Wooded pasture habitats are today forest edges around open fields, forest interior and historical pasture islands. The field study was carried out in 2009 from June to August on 35 islands; three farm islands and 32 satellite islands. The islands were inventoried in a random order. Ten 1m x 1m sample plots were evenly distributed over each habitat per island avoiding the shore with at least 5 m. In case of more than one field the sample plots were distributed evenly among fields. Total species richness (local species pool) per habitat was recorded by walking over the habitat in an even stride per hectare and all present vascular plant species were noted. To measure species richness per area all vascular plant species present in each sample plot were recorded. A subset of 61 species, typical for Swedish grassland habitats, were selected from a list covering grassland specialist species found in Europe (Krauss et al. 2010). Grassland specialists were defined as species that have their main distribution in semi-natural grasslands and are promoted by grazing. Species nomenclature followed Mossberg & Stenberg (2003).

Statistical analyses

Mean total species richness per habitat (local species pool) and standard deviation was calculated for the seven investigated habitat types. For each habitat type sampled, we computed three measures of diversity: i) fine-scale diversity ($\alpha_{ftp}$), ii) large-scale diversity
(γ_{div}), and iii) spatial turnover (β_{div}). Fine-scale and large-scale diversities were computed as the mean number of species per sampling plot (1m²) and the total number of species per ten sampling plots (10 × 1m²) respectively. We used Harrison’s (Harrison et al. 1992) beta diversity measure

\[ β_{div} = \left(\frac{γ_{div}}{α_{div}} - 1\right)/(N - 1) \]

where \( N \) = the number of sampling units used to compute \( γ_{div} \) to measure spatial turnover in species composition. This measure simply put Whittaker’s original beta diversity measure on a standardized scale that range from 0 (no compositional difference between sampled) to 1 (each sample is completely different from each other). Since the distribution of data did not conform to the assumptions of homogeneity of variance and equal sample size between groups a non-parametric ANOVA with Kruskal–Wallis rank sum test followed by non-parametric multiple comparison test of the Behrens–Fischer type was used to test for the significance of difference between means of groups. All statistical analyses were computed with the open source software package R 2.11.1 (R Development Core Team. 2010) and the appropriate additional packages npmc (Munzel 2008).
Results

Landscape change

In the beginning of the 20th century the rural landscape in the Hjälmö-Lådna archipelago had a large proportion of semi-open forest, primarily used for grazing and fuel wood. 10% of the area was meadow 200 years ago whereas 100 years ago most of the meadow had changed to become cultivated fields. The largest change in land-cover occurred between 1900s and 1950s when semi-open forests became increasingly dense. Today there is 1% of semi-open forest left whereas 100 years ago more than 70% were classified as semi-open forest (Table 1). The extent of arable fields was highest 100 years ago with 11% of total land area followed by a decline to 6% in the present landscape. Houses and gardens have increased from less than 1% in 1900s to 8% today but are probably underestimated, as houses are not always visible on aerial photographs and “gardens” in the archipelago are seldom well defined. Almost all meadows became cultivated between 17/1800 and 1900s and disappeared completely before 1950s. The abandonment of arable fields started in 1900s, but fields were kept open which is visible in the class former arable fields both in 1950s and 2000s (Fig. 2).

<table>
<thead>
<tr>
<th>Land use/land cover class</th>
<th>17/1800</th>
<th>1900s</th>
<th>1950s</th>
<th>2000s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arable field</td>
<td>4</td>
<td>11</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>House/garden</td>
<td>0.4</td>
<td>1</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Meadow</td>
<td>10</td>
<td>2</td>
<td>0.1</td>
<td>0</td>
</tr>
<tr>
<td>Former arable field</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>2</td>
</tr>
<tr>
<td>Wetland</td>
<td>0.2</td>
<td>0.3</td>
<td>0.8</td>
<td>0.4</td>
</tr>
<tr>
<td>Grassland</td>
<td>0.7</td>
<td>0.5</td>
<td>1.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Semi-open forest</td>
<td>74</td>
<td>74</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Small open habitats</td>
<td>0.6</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Bedrock with sparse pine</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Closed forest</td>
<td>0</td>
<td>0</td>
<td>67</td>
<td>70</td>
</tr>
</tbody>
</table>

Table 1. The proportion (%) of land use/land cover classes in four time layers from the Hjälmö – Lådna archipelago on the east coast of Sweden. The dominating class in each time layer is shaded.
Figure 2. Flow chart showing the major transitions (in hectares) of the six major land use/land covers classes from 17/1800 to 2000s in the Hjälmö-Lådna archipelago farming system on the east coast of Sweden. The boxes are in proportion to area (ha).

100 years ago there were still 25 farmers in the study area, after the Second World War there were 16, and today there are four farmers left. 40% of the total land area is grazed today, compared with over 80% in 1950s and earlier. The proportions between grazed open fields and forests have not changed much. One example of livestock change is Lådna farm which had 37 cattle in 1906, 25 in 1949 and 30 in 2009. However, the grazing pressure today is highest ever on all farms 0.14 – 0.26 geq/ha today compared to 0.05 – 0.14 geq/ha in 1950s and 0.10 – 0.14 geq/ha in 1900s (Table 2).
Table 2. The proportion of grazed land, grazing pressure measured as grazing equivalents (geq/ha) and number of farms from 1900s to 2000s in the Hjälmö-Lådna archipelago on the east coast of Sweden.

<table>
<thead>
<tr>
<th>Time layer</th>
<th>1900s</th>
<th>1950s</th>
<th>2000s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion grazed land (%)</td>
<td>97</td>
<td>73</td>
<td>39</td>
</tr>
<tr>
<td>(open/closed)</td>
<td>(13/87)</td>
<td>(13/87)</td>
<td>(15/85)</td>
</tr>
<tr>
<td>Grazing pressure (geq/ha)</td>
<td>0.09</td>
<td>0.09</td>
<td>0.17</td>
</tr>
<tr>
<td>Farms</td>
<td>25</td>
<td>16</td>
<td>4</td>
</tr>
</tbody>
</table>

Plant species richness

A total of 353 different plant species were found in the survey. The most species-rich habitats were grazed forest edge and grazed fields, both when all vascular plant species or the sub-selection grassland specialist species were analysed, whereas historical pasture islands were the most species-poor at all spatial scales (Table 3).

The fine-scale diversity ($\alpha_{div}$) (Table 3) for all species was lowest in forest interior (9-10 species/m$^2$); both grazed and formerly grazed. The largest difference in species richness, between open field and wooded pasture, was found for the sub-selection of grassland specialists in grazed habitats, for both fine-scale diversity ($\alpha_{div}$) and large-scale diversity ($\gamma_{div}$); e.g. from 20±5 species/10m$^2$ in grazed field to 6±3 species/10 m$^2$ in grazed forest interior; a decline with 70%. In former grazed habitats the apparent decline was not significant (p>0.05). Fine-scale diversity ($\alpha_{div}$) for all vascular species also declined, but less; from 15±3 species/m$^2$ in grazed field to 10±2 species/m$^2$ in grazed forest interior (a decline with 30%).

Current grazing had a positive influence on fine-scale diversity ($\alpha_{div}$) for grassland specialists in fields (Table 3) and a tendency for higher large-scale diversity ($\gamma_{div}$) for both fields and forest edges. Historical pasture islands (islands that have not been grazed for at least 70 years) had significantly lower fine-scale diversity ($\alpha_{div}$) and large-scale diversity ($\gamma_{div}$). Grazing also had a diversifying effect on species richness as the grazed habitats were significantly different from each other whereas former grazed habitats were not. Also spatial turnover ($\beta_{div}$) was
considerably higher in grazed forest edges and grazed forest interior for all species which can be explained by the influence by both grassland specialists and plants belonging to more forested ecosystems. Spatial turnover ($\beta_{div}$) for grassland species was low in both grazed and former grazed field habitats and former grazed forest interior (Table 3). Former grazed forest interior had significantly lower spatial turnover ($\beta_{div}$) than grazed forest edges for grassland species but not for all species. Field habitats (grazed and former grazed fields) had low spatial turnover ($\beta_{div}$) for both all species and the sub-selection grassland species (Table 3).
Table 3. Mean species richness and standard deviation for seven grassland habitats; both managed and abandoned, in Hjälmö-Lådna archipelago on the east coast of Sweden at four scales; i) local species pool (all species per patch), ii) large-scale diversity ($\gamma_{div}$), iii) spatial turnover($\beta_{div}$), and iv) fine-scale diversity ($\alpha_{div}$) for all vascular plant species (all species) and for grassland specialists (grassland). The most species rich habitat at each scale is shaded.

<table>
<thead>
<tr>
<th>Spatial scale</th>
<th>Local species pool</th>
<th>$\gamma_{div}$</th>
<th>$\beta_{div}$</th>
<th>$\alpha_{div}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All species</td>
<td>Grassland</td>
<td>All species</td>
<td>Grassland</td>
</tr>
<tr>
<td>Grazed field</td>
<td>68±15 $^a$</td>
<td>23±6 $^a$</td>
<td>50±10 $^a$</td>
<td>20±5 $^a$</td>
</tr>
<tr>
<td>(n=18)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazed forest edge</td>
<td>72±16 $^a$</td>
<td>17±7 $^a$</td>
<td>50±12 $^a$</td>
<td>15±6 $^a$</td>
</tr>
<tr>
<td>(n=18)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grazed forest interior</td>
<td>68±12 $^a$</td>
<td>9±4 $^{bde}$</td>
<td>40±7 $^a$</td>
<td>6±3 $^{bdf}$</td>
</tr>
<tr>
<td>(n=13)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Former grazed field</td>
<td>63±10 $^a$</td>
<td>16±6 $^{ad}$</td>
<td>46±7 $^a$</td>
<td>13±5 $^{acd}$</td>
</tr>
<tr>
<td>(n=8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Former grazed forest</td>
<td>66±12 $^a$</td>
<td>13±5 $^{cd}$</td>
<td>42±10 $^a$</td>
<td>10±5 $^{bc}$</td>
</tr>
<tr>
<td>edge (n=8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Former grazed forest</td>
<td>71±12 $^a$</td>
<td>10± $^{bd}$</td>
<td>37±11 $^a$</td>
<td>5±4 $^{bd}$</td>
</tr>
<tr>
<td>interior (n=8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historical pasture</td>
<td>37±8 $^b$</td>
<td>5±3 $^{be}$</td>
<td>20±6 $^b$</td>
<td>3±2 $^{df}$</td>
</tr>
<tr>
<td>island (n=9)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The letters a, b, c, d, e and f indicates significant different groups (p ≤ 0.05), if two habitats have the same suffix (i.e. a) there is no significant difference between the two habitats.
Discussion

200 years of landscape change

The land use in the rural landscape in the archipelago has undergone dramatic changes during the last two hundred years, following the same trend, as elsewhere in Europe, with loss of traditional managed landscape elements. However, much of the structure at present resembles the traditional landscape 100 years ago, as livestock today still graze a multitude of environments; fields, forest edges, shores, wetlands and pine forest on rocky ground, and are not restricted to fenced-in fields. Only parts of the islands are fenced off, primarily around the aggregations of summer houses. The result is a mixture of open and wooded habitats although to a lesser extent than 100 years ago. The forest has become more closed, more land is built upon and meadows have become rare. In the beginning of 1900 the trade with firewood from islands in the archipelago (Hedenstierna 1949; Quist 1949) was a significant source of income, which most likely lead to partially open forests. In addition to grazing the custom to cut shrubs and branches to get winter fodder also kept the forests open. Photographs from at least two of the islands from 100 years ago and descriptions in literature (Hedenstierna 1949) show the islands as fairly open. The shift from a landscape managed for crops and grazing to a landscape characterized by numerous leisure homes began in the decades before 1950s. The number of farms have declined dramatically during the last 100 years, and today the grassland management is a result of conservation action rather that to produce food. All historical pasture islands have been abandoned, as these islands are smaller in size, thus they were abandoned first, when farming decreased in the area during the 20th century. On larger satellite islands grazing management keep the former cultivated fields open to a great extent, whereas on abandoned islands succession has led to overgrown fields and a compact and thick grass sward. The present four farmers keep on grazing 10 satellite islands, besides grazing the
farm islands too. Farmers today have also become more specialized regarding livestock, in 1910 all farmers had horses, cattle and sheep, but in 2009 only one farmer had more than one kind of animals and the other farmers had either sheep or cattle and no horses. The livestock is moved between islands by boat during the summer months.

The importance of grazing

The grazed habitats in this study; former arable fields and wooded semi-natural pastures, are not very species-rich compared to semi-natural grasslands on the mainland. The most species-rich habitat is grazed former arable fields with an average of 15 plant species /m² which is comparable to the same type of habitat on the mainland (Cousins 2009). However, we would have expected more species in grazed wooded pastures as these have been grazed for 200 years and have not been fertilised with artificial fertilisers. There are several plausible explanations to this relative low species richness. First the rural landscape in the archipelago is relative recent. The first farms were only established around 400 years ago, thus the grassland management has existed during a fairly short period too. For comparison, species-rich semi-natural grasslands on the mainland have been managed as grasslands for more than 1000 years (Widgren 1983; Eriksson et al. 2002). Many typical grassland plants are dispersal limited (Ozinga et al. 2009) thus it might not have been enough time for species to colonise. Furthermore, because it is an archipelago the dispersal is likely to be even more restricted, compared to the mainland. Considering this, the species-richness of the former arable fields cannot be considered particularly low. Many of them have been ploughed during the last 50 years so we can expect a continuous increase of species with time (Cousins & Lindbärg 2008), as long as they are kept open with grazing, thus the former arable fields are still important habitats to maintain the diversity of the landscape in the archipelago.

Species richness can be explained by grazing history, particularly for the sub-sample of grassland specialists. Not surprisingly, more grassland specialists are found in open
habitats than in forested habitats, and most important are grazed fields with a mean of 7 grassland specialists / m². This implies that keeping the fields grazed is important also for the sub-group grassland species as soon after grazing ceases species are lost. At the fine-scale \((\alpha_{div})\) we found significant differences depending on habitat. However, for non-grazed habitats the numbers of grassland specialist species become so small (2-5/m²) that no significant difference is detectable. Spatial turnover \((\beta_{div})\) is one measure of how homogeneous a habitat is and the result showed a low spatial turnover \((\beta_{div})\) in both grazed and former grazed fields, especially for grassland species, which indicate that few new species were added when the area was increased. The highest beta diversity for all species was found in grazed forest habitats; one explanation could be that grazing and movement of grazers between the habitats adds grassland species to the forest ecosystem. The environment is also more heterogeneous in grazed forests habitats with a higher degree of local variation in for example soil-types, wetness and interaction with shrubs and tree-species. It is clear that when grazing ceased the landscape became more homogeneous and diversity declined which is in concordance with results from previous studies (Cousins 2009; Krauss et al. 2010).

More than 50% of the land used for grassland management has been lost during the last 50 years. The grazing pressure on the remaining land is higher than ever, and this could be positive for species richness that is associated to grazed habitats. However there is an important difference in the contemporary landscape compared to the managed grassland 50 years ago (beside the land that are not used for grazing anymore), namely that livestock grazed former arable fields and not only semi-natural pastures. More live-stock would be preferable so that more islands and more forested habitats could be grazed, but at present the limitation lies within the manure handling (local farmer; personal communication). At the moment there is not enough arable land is available to spread the manure produced during winter. This is a practical dilemma that needs to be solved. Another conservation measure
would be to carefully open up parts of the denser grazed forest by selectively cutting down trees and thereby improve the habitat for species demanding habitats with more light. Most conservation and restoration efforts have so far focused on species-rich grasslands at a local scale. Our results suggest that grazing is important also in species-poor landscapes and that these results can be an aid in protecting species-richness also in other landscapes. For example, extensive grazing on large rangelands (Kumm 2003; Kumm 2004) encompassing a mosaic of semi-natural grasslands, deciduous forest, ex-arable fields and other small grassland remnants, might greatly contribute to the diversification of the landscape. Grazing has other positive effects on plant diversity as grazers aid dispersal of species between habitats and thereby increase colonisation and diversity in total (Auffret 2011; Auffret et al. submitted ms).

Implications for grassland management in rural landscapes

So far, most studies concerned with plant species diversity have focussed on landscapes with species rich habitats. However, it is important to compare different landscapes with each other to be able to understand the underlying processes influencing species richness in anthropogenic systems, not only diversity “hot-spots”. To investigate species diversity at different scales, here alpha, beta and gamma diversity, give a deeper understanding how processes, such as grazing, influence plant species richness. Our study system, in the Swedish archipelago, has been designated as important for cultural heritage and for biodiversity and the remaining structure is still in many ways resembling the historical landscape. Nevertheless it will probably change in the near future if not measures are taken to financially support the still active farmers.

The conclusion is that low pressure grazing can contribute to biodiversity at all scales; within communities, between habitats and ecosystems, also in species-poor landscapes. In this study we show that grazing increase plant diversity in a heterogeneous landscape and ceased grassland management is negative. To prevent further loss of biodiversity it is important to
keep fields and forest edges open, and therefore it is important for farmers willing to keep grazers in heterogeneous pastures can be able to keep tree densities above EU regulations and still get subsides.

Acknowledgements

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How does variation in landscape context and management history structure plant diversity in grassland communities?

Reto Schmucki*, Josefin Reimark, Regina Lindborg and Sara A. O. Cousins

Abstract

Change in landscape composition and management are two factors that can affect plant diversity and assemblage at various spatiotemporal scales. Although evidence indicates that plant communities are open systems linked through dispersal, most studies on diversity change are still focused on sets of similar habitats depicting the landscape as a binary template and eluding potential effects of adjacent habitats and landscape context on plant diversity. In this study, we used a system of 25 landscapes distributed across 22 islands of the archipelago, on the east coast of Sweden, to examine the effect of landscape context and management history on plant diversity and species composition in grassland communities at local and regional scale. Analysis of species composition in pairs of grazed field and wood pasture revealed the importance of habitat quality and the positive effect of spatial proximity on compositional similarity between contrasting habitats. Structural equation models show that lower proportion of open land and reduced grazing intensity induce a shift in species composition, with no detectable effect on small-scale diversity in grazed field, but significant decline in both small-scale diversity and spatial turnover in adjacent wood pasture. Compositional shift induced by variation in landscape context and management history was correlated to the response of grassland specialists. This pattern was also detected at the landscape scale, suggesting that species composition is influenced by inflow from adjacent habitats affecting species coexistence and the capacity of communities to track biotic and abiotic changes across space and time. Our study highlights the importance of analyzing different components of diversity as species richness used as an aggregate measure of diversity may fail to detect structural change in species assemblage. We stress the importance to consider spatial and temporal heterogeneity within and across habitats when assessing and managing plant diversity in dynamic landscapes.

Keywords: archipelago, Baltic Sea, dispersal, disturbance, grassland, grazing intensity, environmental heterogeneity, historical ecology, metacommunity
**Introduction**

Plant diversity patterns are structured by ecological processes operating at multiple scales over space and time (Wilson 1992, Ricklefs 2004, Harrison and Cornell 2008). Consequently, changes in landscape composition and habitat configuration can have major impacts on the processes shaping and maintaining species diversity in plant communities. Although species coexistence and density is often related to local mechanisms affecting the performance of individuals and local populations (Bengtsson et al. 1994), there is a growing recognition of the importance of dispersal between communities in adjacent habitats (Leibold et al. 2004).

Theoretical models show that environmental heterogeneity and dispersal are major determinants of species diversity at both local and regional scales (Loreau and Mouquet 1999, Mouquet and Loreau 2003, Mouquet et al. 2006). In spite of these developments, the influence of environmental heterogeneity and dispersal on species assembly remains unresolved in real landscapes where their relative importance can vary across systems and be modulated by habitat quality and spatial configuration (Cottenie 2005, Chisholm et al. 2011). An additional challenge is that the effect of configuration is often confounded with variation in habitat quality and management history (Krauss et al. 2003, Roschewitz et al. 2005). Yet, understanding the influence of landscape context, habitat quality, and management history on species assemblage and diversity patterns across scales has far-reaching implications for land management and restoration planning in a world dominated by environmental change.

In northern Europe, semi-natural grasslands covered a large proportion of the
agricultural landscape until the 19th century. Over the last 100 years, however, the extent of these habitats has dramatically declined, mainly as a result of intensification of agricultural activities and cessation of extensive grazing management (Eriksson et al. 2002, Poschlod and WallisDeVries 2002). Most remnant grassland habitats are today restricted to small and isolated patches that have become increasingly important components in agricultural landscape by providing refuge for many taxa, especially habitat specialists (Söderström et al. 2001). Long history of continuous and extensive grazing management partly explains the exceptionally high diversity of plant species found in semi-natural grasslands (Bruun et al. 2001). Although semi-natural grasslands are characterized by high small-scale diversity, species assemblages in these habitats often show little spatial turnover (Cousins and Eriksson 2002). Understanding the factors that structure local diversity and determine compositional turnover can provide insights into the mechanisms shaping and maintaining diversity across scales and habitats.

Environmental heterogeneity and species-area relationship underlie most classical explanations of species diversity patterns, but dispersal mediated processes like migration from adjacent patches with different local dynamics can have important effects on diversity by promoting species coexistence and reducing local and regional extinction risk (Levine and Murrell 2003, Myers and Harms 2009). This is supported by recent studies that show how composition and configuration of the surrounding landscape can influence species assemblage and play a key role in maintaining plant diversity in grassland communities (Öster et al. 2007, Cousins and Aggemyr 2008, Brückmann et al. 2010). One way to evaluate the
effect of landscape context and management history on plant diversity is to partition
diversity into its $\gamma$, $\alpha$, and $\beta$ components (see details under *Diversity estimates*), a
fundamental method to study diversity patterns across scales and infer the
underlying processes (Anderson et al. 2011).

Most studies that examined the effect of landscape context on plant diversity
used a patch-based approach focusing on single rather than multiple habitat types.
Yet, accumulating evidence show that grassland species can inhabit various habitats
in former grazed landscapes (Cousins and Eriksson 2001, Dahlström et al. 2010). By
not including the effect of adjacent habitats, a single habitat approach cannot
adequately address the complexity of the processes controlling diversity patterns in
complex landscapes. Furthermore, studies generally focus on number of species
alone and without accounting for shifts in species composition (but see Brudvig and
Damschen 2011, Piqueray et al. 2011).

In this paper we examine how variations in landscape context and management
history structure plant diversity in grassland communities across scales and
habitats. We hypothesize that spatial processes determined by landscape context
and management history structure species assembly in grassland communities,
affecting both diversity and composition. Specifically, we investigate the response
of i) species diversity, ii) spatial turnover, and iii) species composition at three
hierarchical scales (i.e. 1-m$^2$, habitat, and landscape). Species assemblage and
diversity patterns are expected to be influenced by variation in landscape context as
this factor sets the template for dispersal and thereby affects diversity and spatial
turnover across scales (Mouquet and Loreau 2002, Mouquet et al. 2006). Similarly,
we expect management history to structure species assemblage within and across habitats (Cousins et al. 2007, Gustavsson et al. 2007). In a first step, we examined the relative importance of spatial contiguity and habitat quality on compositional similarity between communities. Second, we use structural equation models to estimate and compare the direct and indirect effects of variations in landscape context and management history on species diversity and composition in grassland communities.
Methods

Study area

This study was conducted in 25 landscapes distributed across 22 islands, covering an extent of 10 by 13 km of the Stockholm archipelago in the Baltic Sea (midpoint 59° 42' N, 18° 70' E). The whole archipelago consists of approximately 24 000 islands, ranging from small skerries to large islands with permanent residents. Annual precipitation is ca. 500 mm and the mean temperature is 6.4 °C, ranging from -3.1 °C in January to 16.7 °C in July (Alexandersson and Eggertsson Karlström 2001). The size of the studied islands ranges from 3 to 526 ha and the bedrock is composed of granites that are covered by sandy moraine and loamy-silt (Geological Survey of Sweden 1974). Cultivable soils are restricted to narrow depressions along the islands that are dominated by bare bedrock and shallow soils. As a result, the extent of agricultural activities is limited by lack of cultivable soils and more than 72% of the islands are covered by forest today. Pinus sylvestris and Picea abies dominate the forests, whereas the forest surrounding open fields is generally semi-open and deciduous (e.g. < 50% canopy cover with Quercus robur, Betula pendula, Alnus glutinosa and Sorbus aucuparia). Historical records show that the forest was significantly more open in the 17th and the 18th centuries due to extensively grazing and as a primary source of timber and fuel. Today, grazing livestock can move freely between fields and adjacent forests currently used as “wood pastures”. Since 1980, more than 50% of the study area is managed as nature reserve by the Archipelago Foundation in Stockholm County with the objective to protect biodiversity and the historical archipelago farming system, including traditional grazing management.
**Landscape data and vegetation survey**

A GIS-model with three time-layers covering the entire study area was constructed based on digitized cadastral maps from 1906 and 1952, and aerial photographs from 1958 and 2004. This period corresponds to important changes in agricultural land management in Sweden, including abandonment and cessation of grazing (Cousins 2009). We selected 25 non-overlapping landscapes, hereafter called sites, of 500 meters radius with a field and an adjacent wood pasture in its centre. For each sites, we calculated the proportion open habitats in 1950 and 2004 and interviewed the landowners about cultivation history and current stocking rate of cows and sheep. Grazing intensity was estimated from the weighted sum of grazing animals, using grazing equivalence to standardize across livestock categories (Dahlström 2008).

In each of the 25 sites, we sampled the grassland vegetation in field and adjacent wood pasture, focusing on the first 50 meters in wood pasture. In each site, 10 plots (1-m²) were randomly distributed within each habitat; avoiding bedrock outcrops and 5 meters along the edges of each habitat (i.e. 10 m buffer where the habitats meet). Between June and August 2009, we recorded all vascular plants rooted within the set of 500 plots. In addition, we recorded total species richness per habitat by inspecting each site with an equal sampling effort per hectare. Since the focus of this study was on grassland plant communities, herbaceous species know to be used to enhance fodder quality in cultivated fields in the archipelago (i.e. *Phleum pratense, Festuca pratensis, Lolium perenne, Trifolium pratense, and Plantago lanceolata*), and tree species were excluded from further analyses. Identification and
nomenclatures follow Mossberg and Stenberg (2003).

**Diversity estimates**

We measured plant diversity in grassland communities at three hierarchical scales: 1-m², habitat, and landscape. Following Jost’s (2007) generalized framework, the number equivalent of Shannon diversity index (i.e. true diversity of order 1) was used to quantify diversity at each scale. This metric has the property of not being disproportionately sensitive to neither rare nor common species. For each habitat, we first quantify fine-scale diversity ($\alpha$-diversity$_{1m^2}$) from the effective number of species per 1-m² derived from the 10 sampling plots. Second, we estimate the total diversity per habitat ($\gamma$-diversity$_{H}$) from the total species inventory, using plot frequency as abundance measure. At the landscape scale, species diversity ($\gamma$-diversity$_{L}$) was computed from total species inventories collected in both field and wood pasture. We estimated compositional change over space by computing the spatial turnover within habitat ($\beta$-diversity$_{1m^2}$: between 1-m² plots) and within landscape ($\beta$-diversity$_{L}$: between adjacent habitats), using the sampling plots and the total inventories, respectively. Consistently with the measures of $\alpha$ and $\gamma$-diversity, we estimated spatial turnover ($\beta$-diversity) from the effective number of compositional units (CU$_E$) sampled in space (Jost 2007).

**Statistical analysis**

To test for difference in species diversity and composition similarity between adjacent field and wood pasture, we conducted pairwise $t$-tests at two scales: 1)
average species density per 1-m² and 2) total diversity per habitat. The effect of spatial contiguity and habitat type [environmental conditions] on compositional similarity was tested by contrasting the observed similarity between pair of adjacent habitats with reference distributions generated through randomization. We used the Horn index of overlap (Eq. 23; Jost 2007) as measure of pairwise similarity, a metric derived from the beta diversity of order 1 and that is not disproportionally sensitive to rare and common species and independent of alpha diversity (Jost 2007). Reference distributions where generated under three null hypotheses: similarity between 1) contrasting and discontinuous habitats, 2) discontinuous fields, and 3) discontinuous wood pastures. Each reference distribution was build from 1000 averages of similarity measures, each calculated from 25 pairs of communities randomly paired by resampling with replacement from the specific stratum (i.e. 1: field-wood pasture, 2: field-field, and 3: wood pasture-wood pasture), while controlling for self-pairing. For each reference distribution, we used the percentile method to define the 95% confidence interval around the mean. This analysis was computed both for total species assemblage and for a subset species containing only grassland specialists. Grassland specialist species were identified from an exhaustive European list of grassland specialized species (Krauss et al. 2010) and lists of species known to be highly associated to semi-natural grasslands in Sweden (Ekstam and Forshed 1996, Lindborg 2007).
**Structural equation model**

We used structural equation modeling (SEM) to investigate the direct and indirect effects of variations in landscape context, spatial distance, and management history on species diversity and composition. SEM provides a rigorous framework to evaluate and compare multivariate hypotheses relating changes in landscape context and management history to variations in diversity component that structure plant communities across scales (Grace 2006). Using a confirmatory approach, we estimated the fit of two conceptual models defined at both habitat and landscape scales (Fig. 1). At the habitat scale, our model tests whether variations in species composition and components of diversity (i.e. \( \alpha \), \( \beta \), and \( \gamma \)) are controlled by variations in landscape context, distance between sampling plots, and management history (i.e. plowing). We defined a comparable model at the landscape scale, testing for linear relationships between variations in landscape context and management history with changes in species composition and component of diversity (\( \beta \) and \( \gamma \)) measured at the landscape scale. At the landscape scale, however, distance between sampling plots was hypothesized to affect total diversity directly rather than through its effect on turnover between habitats (i.e. \( \beta \)-diversity\(_{[L]} \)). We expected the later to be directly controlled by variations in landscape context. In each SEM, landscape context was modeled as a latent variable associated with three manifests: 1) the grazing intensity and 2) the current proportion of open land and 3) in the 1950s. All other variables were modeled from unique indicators, with no measurement error specified. Distance between sampling plots was estimated from the median length of the links connecting all plots in a minimum spanning tree.
Graph. Plowing history was defined by the time since the field was plowed and cultivated (1: < 10 years, 2: 10-50 years, and 3: > 50 years). Based on preliminary examination of the bivariate relationships between variables to identify potential nonlinear relationships, we applied arcsin and square-root transformations to proportion of open land and median distance between plots, respectively. Variation in species composition between sites was estimated with principal component analysis (PCA), using the PCA scores of each community along the first axis. We computed 3 independent PCAs (i.e. field, wood pasture, and landscape), using species abundance data adjusted with Hellinger transformation (Legendre and Gallagher 2001).

To further understand the effects of landscape context and management on specific groups of species (i.e. grassland specialist species); we first applied logistic regressions to test for relationships between proportion of grassland specialists and the PCA scores obtained along the first axis. Since the variance explained on the first axis of each PCA was strongly related to change in proportion of grassland specialists (supplementary material), we fitted reduced SEM to investigate the effects of landscape context, spatial distance, and management history on grassland specialist diversity. All diversity measures and statistical analysis, including estimation and fitting of SEM with maximum-likelihood method, were computed in R 2.13.0 (R Development Core Team 2010).
Results

A total of 199 plant species were found, including 40 grassland specialists. In average, we counted $12.4 \pm 0.8$ (± SE) and $11 \pm 0.6$ species per $1\text{m}^2$ in field and wood pasture, respectively. Based on paired t-tests, $\alpha$-diversity$_{[H]}$ measured in field was significantly higher than in adjacent wood pasture ($t$=2.06, df=24, $P$=0.05). This difference in small-scale diversity, however, did not translate in difference
between $\gamma$-diversity$_H$ measured in field = 44.6±1.3 and adjacent wood pasture = 45.4±1.7 (paired- $t$=-0.34, df=24, P=0.74). Randomization tests indicate higher compositional similarity between grassland communities found in adjacent habitats than expected between pairs of non-adjacent field and wood pasture (Fig. 2 a). In contrast, communities sampled in non-adjacent habitats with similar conditions showed comparable and higher compositional similarities then what we observed between adjacent habitats with contrasting conditions. The effect of habitat quality on species assemblage was particularly important in wood pastures where compositional similarities were highest and showed relatively small variance (Fig. 2 a). Interestingly, similarity observed between communities sampled in contrasting habitats that are adjacent was not significantly different from similarities computed between fields distant from each other. We observed similar patterns for grassland specialists, except that similarity values showed less variation among strata and that the values computed between wood pastures was not significantly different from similarities observed between adjacent habitats with contrasting conditions (Fig. 2 b).

Structural equation models specified at the habitat scale showed reasonably good fit to our data when accounting for all species, with chi-squares of 29.21 and 25.42 with 22 degrees of freedom, giving p-value of 0.14 and 0.28 and in field and wood pasture, respectively (Fig. 3). In wood pasture, SEM shows better fit than in field and $\gamma$-diversity$_H$ was mainly controlled by variation in $\beta$-diversity$_H$. This contrast
Figure 2. Average similarity (vertical dashed line) between pairs of communities sampled in field and adjacent wood pasture computed for (a) all species and (b) grassland specialists. Three reference distributions for average similarities between grassland communities were constructed from 1000 iterations of randomly paired communities resampled within specific stratum: 1. field–wood pasture (dashed line), 2. field–field (solid line), and 3. wood pasture–wood pasture (dash-dotted line). For each distribution, shaded area refers to 95% confidence intervals.
Figure 3. Structural equation models fitted on grassland communities in (a) wood pasture and (b) field. Solid arrows indicate significant relationships and dashed arrows refer to non-significant paths. Estimates, standard errors (within parentheses) and standardized estimates are listed next to each corresponding path. Double-headed arrows refer to covariance estimates. Percentages below PC1 refer to the variance explained by each first component in principal component analysis. Significance p-value level: *** < 0.01; ** ≤ 0.05; * ≤ 0.1; ns > 0.1, CFI: comparative fit index, RMSEA: root mean square error of approximation.
with the relationship observed in field where $\gamma$-diversity$[H]$ was mostly influenced by variation in $\alpha$-diversity$[H]$. While total diversity found in field was positively related to the proportion of open land in the surrounding landscape and the grazing intensity, neither $\alpha$-diversity$[H]$ nor $\beta$-diversity$[H]$ were directly associated to variations in landscape context and distance between sampling plots. In wood pasture, however, change in landscape context manifest by increased proportion of open land and enhanced grazing intensity significantly increased the number of species per 1-m$^2$. In contrast with field, $\beta$-diversity$[H]$ measured in wood pasture increased with distance between sampling plots. In both habitats, the landscape context was mainly determined by variation in current proportion of open land, which showed strong collinearity with the proportion of open land in 1950.

In both field and wood pasture, species composition was significantly related to variation in landscape context as the proportion of grassland specialists declined with reduced area of open land and lower grazing intensity. Not surprisingly, species composition in field was also controlled by time since plowing, with increasing proportion of grassland specialists with time. This effect, however, was not observed in wood pasture where species composition was independent of the time since adjacent field was plowed. Accordingly, our model better explained the variation in species composition within field where the $R^2$ for this variable was 0.84 compared to 0.40 in wood pasture.

Diversity patterns observed for grassland specialists were in line with the compositional changes described in each habitat (Table 1). In field and wood
pasture, \(\alpha\)-diversity\(_{[H]}\) of grassland specialists was positively related to variations in landscape context. In both habitats, variations in \(\gamma\)-diversity\(_{[H]}\) of grassland specialists was mainly determined by \(\alpha\)-diversity\(_{[H]}\) and to a lesser extent by \(\beta\)-diversity\(_{[H]}\). This result contrasts with the diversity structure observed from the total community in wood pasture.

At landscape scale, \(\gamma\)-diversity\(_{[L]}\) of the total community was directly associated to variations in landscape context, but also indirectly through the effects of increased distance between sampling plots and higher \(\beta\)-diversity\(_{[L]}\) between adjacent habitats (Table 2). When the entire community was analyzed, increased proportion of open land and higher grazing intensity significantly increased \(\beta\)-diversity\(_{[L]}\) between habitats. This relationship, however, was not significant for the subset of grassland specialists (Table 2). On the other hand, \(\gamma\)-diversity\(_{[L]}\) of grassland specialists was positively associated with the proportion of open land and grazing intensity (Table 2). This result is in line with the change observed in species composition caused by variations in landscape context. At the landscape scale, species composition was also associated to management history as time since plowing positively affected both diversity and proportion of grassland specialists. Thus, plowing history affected species composition at the landscape scale, but this did not translate in detectable changes in total species diversity (Table 2).
Table 1. Results of structural equation model (SEM) fitted with Maximum Likelihood method on component (γ, α, and β) of diversity for grassland specialist species in wood pasture and field across 25 sites in Stockholm archipelago.

<table>
<thead>
<tr>
<th>Structural Equation</th>
<th>Wood pasture</th>
<th>Field</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model (SEM)</strong></td>
<td>R²</td>
<td>Estimate (SE)</td>
</tr>
<tr>
<td><strong>γ-diversity[H]</strong></td>
<td>0.90</td>
<td>7.36 * (4.29)</td>
</tr>
<tr>
<td>← Landscape context</td>
<td>2.51 *** (0.36)</td>
<td>0.39</td>
</tr>
<tr>
<td>← β-diversity[H]</td>
<td>2.89 *** (0.35)</td>
<td>0.63</td>
</tr>
<tr>
<td>← α-diversity[H]</td>
<td>- 0.30 ns (0.71)</td>
<td>- 0.04</td>
</tr>
<tr>
<td><strong>Spacing</strong></td>
<td>0.45</td>
<td>0.71</td>
</tr>
<tr>
<td>← Landscape context</td>
<td>8.87 *** (2.24)</td>
<td>0.68</td>
</tr>
<tr>
<td><strong>β-diversity[H]</strong></td>
<td>0.25</td>
<td>0.00</td>
</tr>
<tr>
<td>← Spacing</td>
<td>0.23 *** (0.06)</td>
<td>0.50</td>
</tr>
<tr>
<td><strong>α-diversity[H]</strong></td>
<td>0.36</td>
<td>0.20</td>
</tr>
<tr>
<td>← Landscape context</td>
<td>5.29 *** (0.93)</td>
<td>0.60</td>
</tr>
</tbody>
</table>

| **Landscape context** | | | |
| → Open 2000 (asin)³ | 0.89 | 1.00 (0.00) | 0.94 | 0.75 | 1.00 (0.00) | 0.86 |
| → Open 1950 (asin)   | 0.83 | 0.93 *** (0.05) | 0.91 | 0.71 | 0.94 *** (0.06) | 0.84 |
| → Grazing int. (log) | 0.22 | 5.63 *** (2.02) | 0.47 | 0.32 | 7.50 *** (2.30) | 0.57 |

| **Model Fit** | χ²: 23.79 df: 16 P: 0.09 | χ²: 25.30 df: 16 P: 0.07 |
|              | CFI: 0.95 RMSEA: 0.14 | CFI: 0.95 RMSEA: 0.15 |

CFI: comparative fit index
RMSEA: root mean square error of approximation
a: fixed estimate
p-value level: *** < 0.01; ** ≤ 0.05; * ≤ 0.1; ns > 0.1

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<p>18</p>
Table 2. Results of structural equation model (SEM) fitted with Maximum Likelihood method on components ($\gamma$, and $\beta$) of diversity measured at the landscape scale for all species and grassland specialists across 25 sites in Stockholm archipelago. First axis of the PCA explained 18% of the total variance observed in species assemblage.

<table>
<thead>
<tr>
<th>Structural Equation Model (SEM)</th>
<th>All species</th>
<th>Grassland specialists</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R^2$</td>
<td>Estimate (SE)</td>
</tr>
<tr>
<td>$\gamma$-diversity$_{[L]}$</td>
<td>0.85</td>
<td>56.36*** (24.45)</td>
</tr>
<tr>
<td></td>
<td>← Landscape context</td>
<td></td>
</tr>
<tr>
<td>$\beta$-diversity$_{[L]}$</td>
<td>0.34** (0.17)</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>← Spacing</td>
<td>2.39** (0.99)</td>
</tr>
<tr>
<td></td>
<td>← Plowing history</td>
<td>2.26 ns (2.52)</td>
</tr>
<tr>
<td>Spacing</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td></td>
<td>← Landscape context</td>
<td>10.61*** (2.22)</td>
</tr>
<tr>
<td>$\beta$-diversity$_{[L]}$</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td></td>
<td>← Landscape context</td>
<td>0.34** (0.17)</td>
</tr>
<tr>
<td>Composition (PC1:18%)</td>
<td>0.83</td>
<td></td>
</tr>
<tr>
<td></td>
<td>← Landscape context</td>
<td>-3.12** (0.68)</td>
</tr>
<tr>
<td></td>
<td>← Plowing history</td>
<td>-0.22*** (-0.09)</td>
</tr>
<tr>
<td>Landscape context</td>
<td></td>
<td></td>
</tr>
<tr>
<td>→ Open 2000 (asin)$^a$</td>
<td>0.78</td>
<td>1.00 (0.00)</td>
</tr>
<tr>
<td>→ Open 1950 (asin)</td>
<td>0.64</td>
<td>0.88*** (0.05)</td>
</tr>
<tr>
<td>→ Grazing int. (log)</td>
<td>0.21</td>
<td>5.92*** (2.35)</td>
</tr>
<tr>
<td>Model Fit</td>
<td>$\chi^2$: 30.32</td>
<td>df: 21</td>
</tr>
<tr>
<td></td>
<td>CFI: 0.95</td>
<td>RMSEA: 0.13</td>
</tr>
</tbody>
</table>

CFI: comparative fit index  
RMSEA: root mean square error of approximation  
a: fixed estimate  
p-value level: *** < 0.01; ** ≤ 0.05; * ≤ 0.1; ns > 0.1
Discussion

Landscape context and management history showed an overarching effect on both diversity and composition of grassland species assemblage. While habitat conditions constrain species distribution, our results indicate that grassland communities are substantially influenced by the composition of species assembly in adjacent habitats. This suggests that grassland communities should be studied as open systems linked through reciprocal dispersal and functioning as meta-communities. It is clear that to be able to understand local and regional plant diversity patterns, it is important to analyze local habitat quality together with landscape context and management history. This is particularly relevant for species with traits providing them the capacity to colonize and inhabit multiple habitat types.

Plant species generally found in grassland communities, including grassland specialists, can thrive in both field and wood pasture. Effect of adjacent habitats on species diversity has also been documented in grazed former arable field surrounded by commercial forest plantations (Cousins and Aggemyr 2008) or near semi-natural grasslands (Öster et al. 2009). At the landscape scale, heterogeneity created by mosaic of habitats, coupled with interpatch dispersal, might play a key role in maintaining and restoring diversity in space and time (Ozinga et al. 2009, Brudvig et al. 2009). In this perspective, the area per se of a particular land-cover provides a poor estimate of the potential habitat as adjacent patches can harbor species that can contribute to maintain diversity within local communities and at the landscape scale (Öckinger et al. 2011). Although fine-scale diversity found in semi-natural grasslands is generally reported to vary little over space, habitat area
and spatial heterogeneity have been shown to influence the diversity across scales (Öster et al. 2007), suggesting that local species assemblage results from processes operating at multiple scales such as disturbance and dispersal from regional species pool, both affecting species coexistence and diversity (Questad and Foster 2008). This is supported by our results as small-scale diversity of grassland specialists increases in both field and wood pasture when grazing intensity and the extent of open land in surrounding landscape increased. Admittedly, this result must be interpreted carefully as the proportion of open land observed in our system did never exceed 38% and that the relationship between diversity and area of open land is likely to be hump-shaped and change direction beyond certain threshold where the landscape becomes increasingly homogeneous.

Neighboring habitats with contrasting environmental conditions and management history, grazed field and wood pasture, clearly influenced the structure and the diversity in grassland communities at both local and regional scales. However, the scale at which landscape context influences and structures diversity differed between habitats. Indeed, we found that total diversity in field was mainly the result of accumulation of species at small scale, while in wood pasture the influence of spatial turnover was most important. One explanation for this pattern is the spatial structure of environmental heterogeneity (e.g. topography, soil dept, and light conditions) in wood pasture. While coarse grain variations in environmental conditions can explain the spatial structure observed in species distribution in wood pasture, locally patchy disturbances caused by livestock can structure small-scale diversity by creating small-scale non-equilibrium dynamics and facilitate
establishment processes of dispersed seed (Zobel et al. 2000, Questad and Foster 2007, Myers and Harms 2009). Consequently, variations in species assemblage within habitat is most likely explained by the interplay of these disturbances and the spatial structure of environmental heterogeneity, but also by the landscape context that determine composition and density of dispersed propagules through its effect on species pool.

When the proportion of open land within a landscape was reduced and no longer used for livestock grazing, diversity of grassland specialist declined significantly in both field and wood pasture. In wood pasture, however, loss in grassland specialists was not offset by colonization of non-specialist species as in neighboring fields. This stresses the importance to examine the impact of land-use change and habitat loss not only on species richness, but also on composition and abundance. An explanation for the difference in the response of non-specialist species in wood pasture is that small-scale diversity is limited by environmental and biotic constraints. On the other hand, grassland communities in field might be more open to invasion (Eriksson et al. 2006), and thereby, more affected by increasing inflow of non-specialist species from surrounding sources. This pattern also suggests a shift in dominance where specialist species become locally extinct and are progressively replaced by generalist species that increase their dominance and evenness over the landscape (Lindborg et al. 2011). Accordingly, we found that species assemblages in field and wood pasture became more similar as the proportion of open land in the surrounding landscape declined. This was mainly related to species already found in wood pasture invading and becoming increasingly dominant in adjacent field,
possibly resulting from reduced grazing pressure. In our system, grazing intensity was closely related to the proportion of open land available and therefore not randomly distributed across sites. This made it difficult to disentangle the effects of decline in habitat area and change in management regime. However, it is reasonable to expect grassland specialists to decline more rapidly in small habitat and succession to be faster as density of adjacent sources will influence the dynamic of local patches. This raises important questions about the difficulty of estimating extinction debt in complex landscapes and about the value of using species richness without considering shifts in species assemblage within and across habitats (Kuussaari et al. 2009, Jackson and Sax 2010).

**Conclusions**

When management goals are to maintain diversity at landscape scale, it is necessary to account for the potential contribution of adjacent habitats in maintaining species diversity and controlling species coexistence (Lindenmayer et al. 2008). Because changes in landscape context affect species assemblage in different ways across habitats, several aspects of diversity must be examined to understand the processes structuring plant communities in heterogeneous landscapes. We provide clear evidence that subsets of species respond differently to change in landscape context and management history as dependence on these factors varies among species. Our study also emphasized that species richness used as an aggregate measure of diversity may fail to detect diversity response to land use change as local species loss can be shaded by arrival of species that might alter local coexistence and affect regional diversity over time.
Acknowledgements

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Appendix 1. Results of logistic regressions predicting occurrence of specialists in grassland communities sampled in wood pasture (solid line), field (dashed line), and at the landscape scale (dotted line) from the scores on the first component of principal component analysis computed on vegetation from 25 sites distributed across 22 islands in Stockholm archipelago.