Plant community assembly and biodiversity: a spatio-temporal perspective

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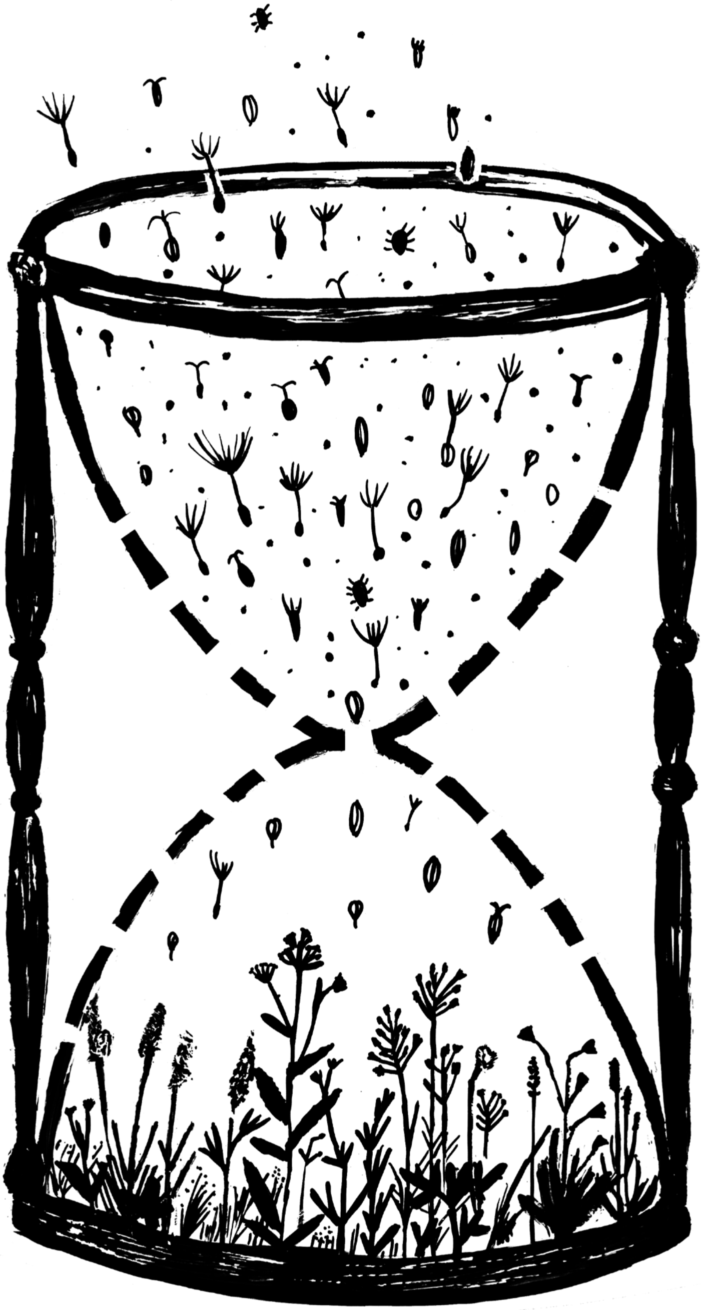

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Abstract

Biodiversity, the variety of life at all organisational levels from genes to ecosystems, affects ecosystem processes and therefore the goods and services ecosystems provide. More research is needed to provide new insights into biodiversity changes and the processes that drive these changes, in order to formulate effective policy and conservation measures to stop the ongoing biodiversity loss. In this thesis, I focus on spatial and temporal changes in different aspects of plant biodiversity and examine the driving forces that generate and maintain observed biodiversity patterns. Multiple facets of biodiversity (taxonomic, phylogenetic, functional) were characterized in semi-natural grasslands (in plots of 0.5 × 0.5 and 2 × 2 m, and whole grassland polygons). The extent to which the present-day and historical characteristics of the sites and their surrounding landscape explain the current diversity patterns was quantified. Temporal changes in the multiple facets of diversity, and assembly processes that drive these changes, were investigated along a more than 300 year long chronosequence representing an arable to semi-natural grassland succession. Both grassland plant species richness and functional trait diversity in grassland sites were to a large extent explained by the land use history of the sites and the availability of grassland habitat in the surrounding historical landscape. It appears that not only is there a delayed loss of species diversity in response to landscape fragmentation ("extinction debt") but that there is also a delayed decline of functional diversity in response to ongoing habitat destruction (i.e. a "functioning debt") that will potentially generate a time lag in the changes in ecosystem attributes. Quantification of the linkages between the distribution and diversity of dispersal and persistence traits and current and historical properties of the grassland sites and their surrounding landscape revealed that long-distance dispersal potential as well as the diversity of different dispersal and persistence strategies within present-day grassland communities was mainly determined by the local management history and landscape history. Long-distance dispersal by wind and animals no longer appears to be contributing to the colonization of the remaining fragments of habitat within the increasingly fragmented modern landscape, and long-term persistent species are likely to dominate the grassland communities in the future. Whereas many long-distance dispersed species can still persist locally in the presence of grazing disturbance, grazing management may also promote the diversity of different dispersal and persistence strategies, but only in sites that were well connected to grassland areas in the past. The extent to which grassland management strategies can maintain a high diversity of dispersal and persistence strategies, and thereby the capacity of a plant community to buffer environmental change, will depend on the context of the site within the historical surrounding landscape. Comparative analysis of taxonomic, phylogenetic and functional diversity at different stages of arable-to-semi-natural grassland succession demonstrated that community assembly during secondary grassland succession was deterministic with respect to species traits, suggesting that it may be possible to predict changes in biodiversity, and associated alterations in ecosystems functioning in future environments, on the basis of species functional traits. Taxonomic, phylogenetic and functional diversity showed contrasting patterns of change over time. Short-term grazing management (5-50 years) promoted species richness, but did not enhance phylogenetic or functional diversity. Only long-term grazing management, over more than 270 years, promoted phylogenetic and functional diversity without further increases in species richness. I conclude that (a) multiple facets of biodiversity should be considered in order to more realistically assess the full dimensions of biodiversity loss resulting from human-driven environmental changes, (b) history is a major determinant of biodiversity, and (c) the simultaneous consideration of multiple facets of biodiversity can provide new insights into the processes that shape communities.

Key words: dispersal, functional diversity, landscape fragmentation, land use history, life-history traits, null model, phylogenetic diversity, semi-natural grasslands

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Plant community assembly & biodiversity

A spatio-temporal perspective

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Abstract

Biodiversity, the variety of life at all organisational levels from genes to ecosystems, affects ecosystem processes and therefore the goods and services ecosystems provide. More research is needed to provide new insights into biodiversity changes and the processes that drive these changes, in order to formulate effective policy and conservation measures to stop the ongoing biodiversity loss.

In this thesis, I focus on spatial and temporal changes in different aspects of plant biodiversity and examine the driving forces that generate and maintain observed biodiversity patterns. Multiple facets of biodiversity (taxonomic, phylogenetic, functional) were characterized in semi-natural grasslands (in plots of 0.5 × 0.5 and 2 × 2 m, and whole grassland polygons). The extent to which the present-day and historical characteristics of the sites and their surrounding landscape explain the current diversity patterns was quantified. Temporal changes in the multiple facets of diversity, and assembly processes that drive these changes, were investigated along a more than 300 year long chronosequence representing an arable-to-semi-natural grassland succession.

Both grassland plant species richness and functional trait diversity in grassland sites were to a large extent explained by the land use history of the sites and the availability of grassland habitat in the surrounding historical landscape. It appears that not only is there a delayed loss of species diversity in response to landscape fragmentation ("extinction debt") but that there is also a delayed decline of functional diversity in response to ongoing habitat destruction (i.e. a "functioning debt") that will potentially generate a time lag in the changes in ecosystem attributes.

Quantification of the linkages between the distribution and diversity of dispersal and persistence traits and current and historical properties of the grassland sites and their surrounding landscape revealed that long-distance dispersal potential as well as the diversity of different dispersal and persistence strategies within present-day grassland communities was mainly determined by the local management history and landscape history. Long-distance dispersal by wind and animals no longer appears to be contributing to the colonization of the remaining fragments of habitat within the increasingly fragmented modern landscape, and long-term persistent species are likely to dominate the grassland communities in the future. Whereas many long-distance dispersed species can still persist locally in the presence of grazing disturbance, grazing management may also promote the diversity of different dispersal and persistence strategies, but only in sites that were well connected to grassland areas in the past. The extent to which grassland management strategies can maintain a high diversity of dispersal and persistence strategies, and thereby the capacity of a plant community to buffer environmental change, will depend on the context of the site within the historical surrounding landscape.

Comparative analysis of taxonomic, phylogenetic and functional diversity at different stages of arable-to-semi-natural grassland succession demonstrated that community assembly during secondary grassland succession was deterministic with respect to species traits, suggesting that it may be possible to predict changes in biodiversity, and associated alterations in ecosystems functioning in future environments, on the basis of species functional traits. Taxonomic, phylogenetic and functional diversity showed contrasting patterns of change over time. Short-term grazing management (5-50 years) promoted species richness, but did not enhance phylogenetic or functional diversity. Only long-term grazing management, over more than 270 years, promoted phylogenetic and functional diversity without further increases in species richness.

I conclude that (a) multiple facets of biodiversity should be considered in order to more realistically assess the full dimensions of biodiversity loss resulting from human-driven environmental changes, (b) history is a major determinant of biodiversity, and (c) the simultaneous consideration of multiple facets of biodiversity can provide new insights into the processes that shape communities.

Keywords: dispersal, functional diversity, landscape fragmentation, land use history, life-history traits, null model, phylogenetic diversity, semi-natural grasslands

List of papers

This thesis is based on the following papers which are referred to by their Roman numerals:

I Reitalu, T., Purschke, O., Johansson, L.J., Hall, K., Sykes, M.T. & Prentice, H.C. (2011) Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialisation. *Journal of Vegetation Science* (in press) DOI: 10.1111/j.1654-1103.2011.01334.x.

II Purschke, O., Sykes, M.T., Reitalu, T., Poschlod, P. & Prentice, H.C. (2011) Linking landscape history and dispersal traits in grassland plant communities. *Oecologia* (in press) DOI: 10.1007/s00442-011-2142-6.

III Purschke, O., Sykes, M.T., Poschlod, P., Michalski, S., Römermann, C., Durka, W., Kühn, I., Prentice, H.C. Current and historical drivers of dispersal trait diversity in plant communities. (Manuscript).

IV Vandewalle, M., Purschke, O., de Bello, F., Reitalu, T., Prentice, H.C., Lavorel, S., Johansson, L.J. & Sykes, M.T. Plant functional responses to local, landscape and historical factors in semi-natural grasslands (Manuscript).

V Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S., Durka, W., Kühn, I., Winter, M., Prentice, H.C. Contrasting changes in taxonomic, phylogenetic and functional diversity during secondary grassland succession (Manuscript).

Papers I and II are reprinted with permission from the publishers.

My contribution to the papers:

Paper I: I had the main responsibility in collecting the species presence-absence data and was involved in the data analysis and the writing of the paper.
Papers II & III: I had the main responsibility for collecting the species presence-absence data and for the writing of the paper. I compiled/derived trait data from data bases and analysed the data.
Paper IV: I was involved in the data analysis and the writing of the paper.
Paper V: I compiled/derived trait data from data bases, analysed the data and had the main responsibility for the writing of the paper.

Contents

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Plant community assembly and biodiversity: a spatio-temporal perspective

Introduction

There is compelling evidence that biodiversity, the variety of life at all organisational levels from genes to ecosystems (Wilson 1988; Gaston 1996; Purvis & Hector 2000), affects ecosystem processes and the goods and services they provide for human well-being (Diaz et al. 2006). Throughout the history of life, biological diversity has been changing constantly, including several mass extinction events (Lawton & May 1995; Benton 2010). Currently, life on earth experiences its sixth major extinction event, with extinction rates 100-1000 times higher than pre-human extinction rates (Pimm et al. 1995). However, while earlier major changes in biodiversity were mainly driven by sudden changes in the physical environment, such as massive volcanic eruptions and asteroid impacts, the current loss of biodiversity is driven by climate change, habitat loss, biological invasions and other negative consequences of human activity (Chapin et al. 2000). More research is needed to provide new insights into biodiversity changes and the processes that drive these changes, in order to formulate effective policy and conservation measures to stop the ongoing biodiversity loss (Magurran & Dornelas 2010).

All aspects of biodiversity, from genetic diversity to the diversity of landscape units, play a role for ecosystem functioning. However, because the phenotypic characteristics (traits) of a species determine its performance, the diversity of functional traits (functional diversity) represents a direct link between changes in community composition and ecosystem processes (Diaz & Cabido 2001; Weiher 2010). Higher levels of functional diversity in plant communities have been shown to increase productivity (Cadotte et al. 2009) as well as to enhance the stability of ecosystems in response to perturbations (Hobbs et al. 2007; Laliberté et al. 2010), and may also affect ecosystem services (Kremen 2005; Mayfield et al. 2005).

In this thesis, I focus on spatial and temporal changes in different aspects of plant biodiversity and scrutinize the driving forces that generate and maintain the observed biodiversity patterns.

Community assembly processes and biodiversity patterns

Elucidating the processes that shape plant communities is essential for the prediction of how biodiversity and ecosystem functioning will be affected by future environmental change. (Götzenberger et al. 2011; Weiher et al. 2011). The assembly of plant species into local communities is driven by both stochastic (trait-neutral; Hubbell 2001) and deterministic processes, which act simultaneously to determine community composition and biodiversity. Deterministic community assembly is often understood as pool-filter-subset concept: species that co-exist in local communities are a subset of the larger (regional) species pool from which they are selected, according to their traits, by a set of hierarchical abiotic and biotic filtering processes (Keddy 1992; Poff 1997). The species (and their traits) that are available in the species pool and the kind of filters determine the range and dispersion of traits in the local communities. Abiotic filters may act at different spatial scales

(Algar et al. 2011) and tend to generate overall trait similarity (trait convergence; Grime 2006), because species share similar adaptations to the physical environment. For example, at larger spatial scales, climate acts as a filter selecting for freezing tolerant plant species in areas that experience hard frosts (Davis et al. 1999). At smaller (local) scales, trait convergence has been demonstrated in sites with higher levels of productivity and/or under severe disturbance (Grime 2006; Pakeman et al. 2011). Biotic filters, such as competition, act on smaller spatial scales where species interact, and tend to generate overall trait dissimilarity (trait divergence). Competition is strongest between species with similar resource use, and will tend to prevent the co-existence of species that have a high level of functional similarity (“limiting similarity”; MacArthur & Levins 1967).

In addition to competition and stress filters, dispersal between communities plays a central role in plant community assembly (Ozinga et al. 2009). Especially in fragmented landscapes, seed dispersal has been demonstrated to limit plant species composition and biodiversity in local communities (Verheyen & Hermy 2001; Adriaens et al. 2007). The degree to which species distributions are dispersal limited depends on the dispersal traits of the species in the larger (regional) geographical species pool, as well as the spatial distribution of suitable habitat. Whereas spatial isolation may act as a dispersal filter at the landscape scale (Hanski 1999; Eriksson et al. 2002), the availability of suitable microsites (gaps), at the local scale, will determine whether seeds can establish once they have dispersed into a site (Grubb 1977; Bullock et al. 1995).

In rapidly changing environments, species often show a delayed response to fragmentation and may persist in the remaining habitat fragments over long periods of time under non-optimal conditions (“extinction debt”; Tilman et al. 1994; Herben et al. 2006), even though the spread of species between sites will be increasingly limited by dispersal in space. The species composition and distribution of the traits in present-day communities is therefore expected to reflect the spatial configuration of colonization sources in the historical landscape and the long-term availability of suitable microsites (Snäll et al. 2003; Lindborg 2007).

Quantification of the linkages between plant functional traits, especially those related to dispersal and persistence, and the current and historical characteristics of the local habitat and its surrounding landscape is likely to greatly increase our ability to predict the effects of a changing environment on the biosphere (McGill et al. 2006).

Temporal changes in biodiversity

Ecosystems are affected by different kinds of disturbances, that may have dramatic consequences for biodiversity (Magurran & Dornelas 2010). After disturbance, succession occurs – a processes in which species are sequentially replaced over time (Clements 1916). The study of temporal changes in biodiversity during succession may allow to assess how biodiversity can be maintained/restored after ecosystem disturbance. Biodiversity is multi-faceted and recent studies emphasize that the assessment of biodiversity changes should not merely focus on species identities but also need to take functional and phylogenetic differences between species into account (Devictor et al. 2010a; Meynard et al. 2011). Both functional and phylogenetic diversity are associated with ecosystem resilience: whereas functional diversity is potentially related to the capacity of an ecosystem to respond to environmental changes (see previous section), phylogenetic diversity reflects the accumulated evolutionary history of a community and therefore reflects the potential to produce new evolutionary options, and to persist, under future environmental changes (Purvis & Hector 2000; Forest et al. 2007). Under the assumption that phylogenetically closely related species share similar traits (i.e. show trait conservatism), and therefore are ecologically and functionally similar, phylogenetic diversity is often used as a proxy for functional diversity. If traits are conserved, phylogenetic diversity may provide a more inclusive measure of functional diversity than measures of functional diversity which are based on a limited set of measurable traits.

Studies of biodiversity changes after disturbance have mainly focussed on diversity within communities (alpha diversity; Laliberté et al. 2010; Letcher 2010). However, biodiversity also has a spatial component, that can be determined by measuring how the community composition changes across a landscape (beta diversity). The assessment of temporal changes in beta diversity after disturbance may reveal insights into whether communities become more similar or dissimilar over time (Fukami et al. 2005; Vellend et al. 2007).

Recent studies (Dinnage 2009; Letcher 2010) have suggested that measuring and comparing taxonomic, phylogenetic and functional (alpha and beta) diversity during succession may provide insights into the processes that generate biodiversity after disturbance. Both stochastic and deterministic processes are likely to be involved in driving community assembly during succession, and their relative importance may change as succession proceeds (Huston & Smith 1987). Deterministic processes include abiotic and biotic filtering and are expected to generate non-random patterns in community composition with respect to species traits. However, the observed ("raw") functional trait diversity measures are of little direct use in the detection of such assembly processes. Observed functional diversity values need to be compared with expected functional diversity values obtained from random communities that were generated using a null model that keeps constant the levels of taxonomic diversity (Gotelli & Graves 1996). Whereas abiotic filtering is expected to generate communities (consisting of functionally similar species) that have a functional diversity that is lower than expected, given the taxonomic diversity, biotic filtering processes such as competition are expected to generate communities (consisting of functionally dissimilar species) with a higher than expected functional trait diversity.

Information on phylogenetic diversity can provide additional information that is not covered by functional diversity (Pausas & Verdu 2010; Pavoine & Bonsall 2011). For example, a situation where phylogenetic diversity is higher or lower than expected, but the functional diversity does not differ from null expectations, suggests that important functional traits may be missing from the analysis. On the other hand, if traits are not conserved, and closely related species do not share similar traits, a non-random pattern of functional diversity, but a random pattern of phylogenetic diversity, indicates that the traits that were used to assess functional diversity are involved in the assembly process.

Aims of the thesis

1) To quantify the extent to which biodiversity in grassland plant communities is explained by historical and current characteristics of the landscape and the local management regime. **(Papers I & IV)**

2) To link the dispersal potential in present-day communities to the properties of the current and historical landscapes. To what extent is the distribution of dispersal and persistence traits, and the diversity of these traits, explained by the historical properties of the landscape? **(Papers II & III)**

3) To assess successional changes in biodiversity after disturbance, and to gain insight into the processes that generate and maintain the observed diversity changes. **(Paper V)**

Methods

Study area

The study area (centred on 56°33’58” N, 16°33’58” E) is situated in the central part of the Baltic Island of Öland (Sweden) and covers approximately 22.5 km² (Fig. 1). The landscape has on overall flat topography and consists of a mosaic of grassland, arable fields and forests. Öland has a long history of grazing that dates back until the early Neolithic (3000-3300 BC). However, the proportion of semi-natural grassland in the study area has progressively declined since the early eighteenth century, from 86% in 1723 to 9% in 1994 (Johansson et al. 2008).

Vegetation data

In the first four studies (Papers I-IV), vegetation was sampled in semi-natural grassland polygons that were classified according to their age (grassland continuity) and previous land use (arable fields, forests or old grasslands) by Johansson et al. (2008). In order to avoid major gradients of edaphic variation, vegetation sampling was restricted to dry grassland vegetation with low levels of eutrophication, containing the grasses Festuca ovina and/or Helictotrichon pratense. Both of these species are widespread in dry and mesic grasslands within the study area and avoid eutrophicated habitats (Prentice et al. 2007). In order to reduce edge effects (see Reitalu et al. 2008), we did not sample the area within a 2 m-wide internal buffer zone along polygon borders. For the first three studies (Papers I-III), presence/absence data were recorded for all herbaceous, vascular plant species (186 species in total), between May and August 2007, in 113 grassland polygons. Plot-scale data vegetation data (Papers I & IV) were collected between May-July 2004 by Reitalu et al. (2008) in 425 (Paper I) and 475 (Paper IV) 50 × 50 cm plots that were positioned randomly within the sampling areas. Each plot was divided into 25 10 cm × 10 cm sub-plots within which the presence/absence of all vascular plant species was recorded.

In the successional study (Paper V), vegetation surveys were carried out in younger grasslands on previously arable sites and in old semi-natural grasslands – representing a chronosequence from arable to semi-natural grassland succession. Each grassland site was assigned to one of four succes-

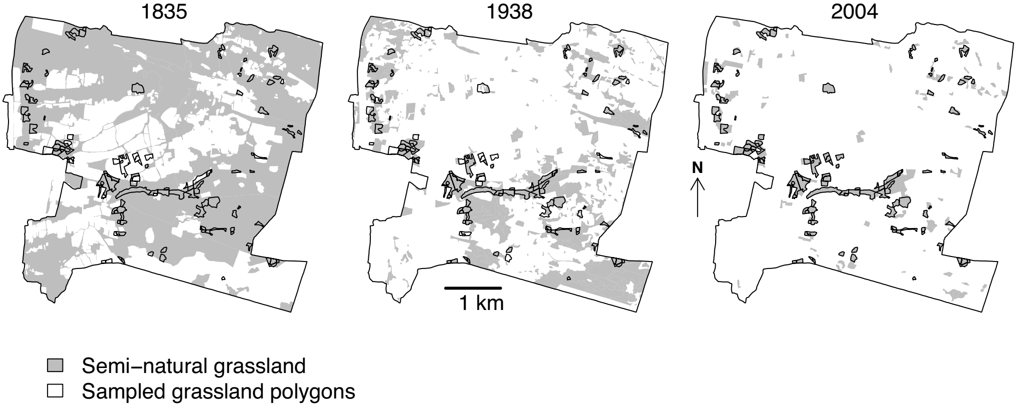

Fig. 1. Land-cover maps of the Jordtorp study area for three time periods (1835, 1938 and 2004). The 113 grassland polygons in which vegetation for the studies in Papers I-III was sampled are indicated.

sional age classes, corresponding to 5-15, 16-50, 51-270 and >270 years of grassland continuity, using GIS-overlay analysis based on historical land-use maps (Johansson et al. 2008). Between May and July 2009, presence/absence data were collected for all non-woody, vascular plant species (234 in total) within 2 × 2 m plots. Each of the four successional stages is represented by 55 plots (n=220 in total).

Local (site) descriptors

For the studies in Papers I-IV, each grassland polygon was assigned to one of four age classes (30, 55, 105 and >275 years), defined as years of grassland continuity before 2004, based on GIS overlay analysis of land-cover/vegetation maps produced from historical maps or aerial photographs by Johansson et al. (2008). Grazing intensity, on a scale of 0 to 4 (ungrazed to well-grazed), was subjectively estimated, on the basis of vegetation height, the presence of grazing animals and recent signs of grazing such as dung/droppings and cropped vegetation (Reitalu et al. 2008). Within each grassland polygon, the total area (ha) was estimated, and the cover of trees (%) was used as a descriptor of light-availability (shading) and litter accumulation (Reitalu et al. 2008). Habitat heterogeneity was quantified by the Shannon-Wiener index based on the proportions (%) of seven different sub-habitats: the cover of trees, the cover of each of the shrub species *Prunus spinosa, Juniperus communis* and *Corylus avellana*, and the proportions of moist areas, eutrophicated areas and tracks.

In Paper V, the amount of within-plot disturbance was characterized by the percentage of bare ground, and total available phosphorus was estimated from mixed soil samples (3-5 per plot) using the Bray 1 method.

Landscape descriptors

Historical and present landscape structure was quantified, within a 200-m (Paper IV) and 300-m (Papers I-III) buffer zone surrounding the edges of the studied grassland polygons (Johansson et al. 2008). Measures of historical landscape structure were based on land cover maps from three different time periods (1800, 1835, 1938). Three kinds of landscape descriptors were used: (1) percentage of grassland habitat (Papers I-IV), (2) percentage of forest (Paper IV) and (3) diversity of the surrounding landscape (Papers I-III), defined by the Shannon-Wiener Index and ten habitat types: semi-natural grassland, alvar grassland, cultivated grassland, other grassland, arable land, closed forest, semi-open forest, hazel scrub, wetland and other land use (classified by Johansson et al. 2008).

Traits

For the studies in Papers II-V we used quantitative information of plant functional traits (continuous and ordinal) that were either measured in the field and in the lab (Paper IV), or compiled from data bases (Papers II, III & V; Poschlod et al. 2003; Kleyer et al. 2008). The traits that were used are potentially important for the species' response to environmental change, and/or are important to ecosystem functioning. The studies in Papers II and III focussed on the following regenerative traits that are related to the plant species ability to disperse and persist: long-distance dispersal potential by wind and animals (epi- and endozoochory), seed bank persistence, adult plant longevity, seed production per ramet and seed mass. Both regenerative and vegetative traits were used in Papers IV and V. The vegetative traits comprised canopy height, reproductive height, lateral spread, toughness, leaf size, specific leaf area, leaf dry matter content and plant life form, and are mainly related to the plant species' competitive ability and the ability to respond to environmental stress.

Phylogeny

Phylogenetic data (in Papers III & V) were obtained from a phylogenetic supertree for Central European Angiosperms (Durka 2002; with updated topology) without branch length information. Branch length information was obtained by dating the internal nodes of the topological tree with the help of an extensive literature survey on published ages of the respective branching events. Missing species (*Helianthemum oelandicum, Oxytropis campestris, Ranunculus auricomus, Sesleria uliginosa)* were added manually.

Diversity measures

Multiple facets of biodiversity (taxonomic, functional and phylogenetic), as well as their within- (alpha) and between- (beta) community components, were calculated.

Species richness (taxonomic alpha diversity) of grassland specialist and generalist species, in 50 × 50 cm plots, as well as in entire grassland polygons, was estimated in Paper I.

In Paper IV, functional trait diversity for single traits was calculated using the Rao index (cf. Lavorel et al. 2008), which is the sum of all pairwise distances between species with respect to their trait values, and measures the extent to which species within a community are functionally different.

Two measures of multivariate-trait diversity (including five dispersal and persistence traits) within grassland sites were assessed in Paper III: a) Functional richness (Cornwell et al. 2006), a measure of the multivariate range of trait values, or the functional space that is occupied by species, and b) Functional divergence (Villéger et al. 2008), a measure of how species are distributed within the functional trait space and of the extent to which the species in a community have distinct or extreme trait values.

In the successional study (Paper V), functional and phylogenetic (alpha and beta diversity) were assessed. For consistency, the functional and phylogenetic diversity indices were calculated using identical methods. Both functional and phylogenetic alpha diversity were characterised by the mean pairwise distance (MPD, Webb et al. 2002) which was calculated from species distance matrices based on either eleven species traits or the branch lengths in the phylogenetic tree (Devictor et al. 2010a). Taxonomic, phylogenetic and functional beta diversity were assessed based on Sørenson's index. For phylogenetic and functional beta diversity, the Sørenson index was defined as the fraction of branch length that is shared between two communities, either in a phylogenetic tree or a functional trait dendrogram (Bryant et al. 2008; Swenson et al. 2011).

Analysis

The studies in Papers I, III and IV used generalized linear models (GLMs) to quantify the relationship between the environmental descriptors (both current and historical) and the different diversity measures. Hierarchical partitioning (Chevan & Sutherland 1991) was used in Paper I to estimate the independent contribution of each of the explanatory variables in the multivariate GLMs. Two-way interactions between the local and landscape descriptors, as well as quadratic effects, were included in the GLMs in Paper III.

Spatial autocorrelation in the model residuals was addressed using simultaneous autoregressive (SAR) models (Kissling & Carl 2008) in Paper IV. In Paper III we accounted for spatial and phylogenetic residual autocorrelation simultaneously, using spatio-phylogenetic eigenvector filtering (Kühn et al. 2009).

Permutation-based fourth-corner analysis (a three-table method) was used in Paper II, to quantify and test the direct linkages between species traits and the environmental conditions of the sites where the species occur (Dray & Legendre 2008).

Various types of null models were used in Papers III and V to assess whether the observed values of functional or phylogenetic diversity were higher or lower than expected from a random draw of species from the regional species pool.

Results and discussion

The response of biodiversity to local, landscape and historical factors

The range of ecosystem functions that a community provides is determined by the diversity of functional traits as well as the diversity of species that carry these traits (Mayfield et al. 2010). The results in Papers I and IV show that the species richness, as well as functional trait composition (communities weighted mean trait values (CWM) and functional divergence (FD)), within semi-natural grassland plant communities are determined by both current and the historical characteristics of the landscape and local the management regime.

Species richness

Significant relationships between species richness and local environmental factors and the structure of the surrounding landscape, both at the present-day and in the past, have been demonstrated in earlier studies (Bruun 2000; Lindborg & Eriksson 2004; Reitalu et al. 2009). However, if species with restricted ecological preferences (specialists) are more strongly affected by environmental change than species that occupy a wider range of habitats (generalists; Pandit et al. 2009; Devictor et al. 2010b; ten Brink & Bruun 2011), the response of species richness to habitat loss and fragmentation is expected to depend on the degree of habitat specialization. Relationships between species diversity and local and landscape factors may also depend on the scale of the study (Weiher & Howe 2003), and may, for example, depend on whether species data were collected in small plots (< 1m²; e.g. Öster et al. 2007; Reitalu et al. 2009) or within entire patches (Bruun 2000; Krauss et al. 2004).

We found that at the scale of the whole grassland polygon (patch), species richness of both specialists and generalists were mainly explained by local habitat characteristics (grassland continuity and grazing intensity; Table 3 and Fig. 2 in Paper I). At the scale of 50 × 50 cm grassland plots, species richness was explained by local habitat characteristics as well as the properties of the surrounding landscape, with specialist species richness being associated with a different set of environmental and landscape variables than the species richness of generalists (Table 3 and Fig. 2 in Paper I).

The positive association between grassland continuity and species richness at the polygon scale suggests that both specialists and generalists have accumulated in the old grassland sites over centuries of grazing management. Species richness increased with higher grazing intensity, suggesting that the abandonment of grazing management is likely to cause decreases in the species richness of both specialists and generalists.

At the scale of 50 × 50 cm plots, the species richness of specialist species was higher in grassland plots that were surrounded by a highly heterogeneous landscape (Table 3 and Fig. 2 in Paper I), suggesting that the negative effects of landscape fragmentation on grassland communities may be compensated for by the input of grassland species from a highly diverse surrounding landscape.

Functional trait responses

Although the impact of local management regime and landscape structure on species diversity is increasingly recognized, few studies have investigated how functional trait diversity (i.e. functional composition) may respond to these different factors (but see Mokany et al. 2008) and historical factors have been included even more seldom into these studies (but see Lindborg 2007; Quetier et al. 2007). In Paper IV we characterized the functional composition within grassland communities with respect to ten plant characteristics (traits) that are potentially related to the plant species' response to environmental changes and/or that may affect ecosystem processes.

The functional trait composition of present-day communities was explained by both current and historical habitat conditions (Table 2 in Paper IV). The significant relationship between historical factors and the community weighted mean trait values (CWM), as well as the functional dissimilarity (FD) in present-day communities, indicates that there is a long time lag in the functional response to landscape fragmentation and habitat loss.

The FD of seed mass, leaf size, lateral spread and natural reproductive height were positively associated with present-day grazing intensity (Table 2 in Paper IV), suggesting that abandonment of grazing management would not only cause declines in species richness (see Paper I) but is also likely to cause a loss of trait diversity, at least in these four traits, and consequently a loss of ecosystem functions that are associated with these traits. The decrease of CWM of reproductive height in response to grazing was accompanied by increases in FD for this trait, suggesting that mean vegetative height may not be a sufficient indicator for grazing intensity.

We also show that the CWM of leaf size and the CWM of lateral spread increased with increasing percentages of shrub cover within the grassland patches (Table 2 in Paper IV). Shrub cover may be related to light availability and may also reflect longer periods of grassland abandonment, and therefore the greater leaf size and lateral spread values are likely to reflect an advanced stage of succession (Kahmen & Poschlod 2004).

The functional composition in present-day communities was not significantly associated with the structure of the current landscape, but instead with the percentage of grassland habitat in the historical landscape (in 1800), indicating that the plots that were surrounded by high amounts of grassland habitat in the past not only are taxonomically more diverse (see Paper I), but are also more diverse functionally.

Our results suggest that both current and historical drivers of changes in biodiversity need to been taken into account in order to develop reliable indicators of biodiversity change.

Linking dispersal potential and landscape history

The ability to disperse and persist determines the response of plant species to environmental changes (Cain et al. 2000; Nathan 2006). Each plant species is potentially dispersed by multiple vectors in space as well as in time, and the diversity of dispersal and persistence traits therefore represents an important aspect of biodiversity that is likely to influence the way in which communities and their associated functions are sustained under future environmental change (Ozinga et al. 2004; Mayfield et al. 2006). But what are the factors that determine the distribution and the diversity of dispersal and persistence traits in plant communities?

If there is a time lag in species' responses to rapid land use change, the dispersal characteristics of species in present-day plant communities are expected to reflect the historical rather than current availability of suitable habitat (Herben et al. 2006). In Papers II and III we show that both the long-distance dispersal traits and the diversity of dispersal and persistence strategies, within present-day grassland plant communities were mainly determined by historical rather than current characteristics of the landscape and the local management regime, highlighting the importance of history as a determinant of dispersal potential.

Dispersal and persistence traits

Our results demonstrate that grassland sites that were surrounded by large proportions of grassland habitat as well as had a long history of continuous grazing management contained plant species that had a high long-distance dispersal (LDD) potential by wind and animals (Figs. 2, 3; Table 2 in Paper II). None of the dispersal traits was associated with the amount of grassland habitat within the current surrounding landscape, suggesting that the colonization of plant species that are dependent on long-distance dispersal is limited within the current landscape. However, we also found that wind dispersal potential was higher in intensely grazed sites, whereas animal dispersal potential increased with decreasing tree cover - although dispersal is limited within the increasingly fragmented landscape, wind- and animal dispersed species may persist locally in sites that are open (less shaded) and disturbed by grazing which creates gaps that are available for establishment. While not associated with the percentage of grassland habitat in the current surrounding landscape, adult plant longevity was significantly higher in sites that were isolated in the past (Fig. 2), indicating that long-term persistent species with the ability to spread clonally show a delayed response to habitat fragmentation.

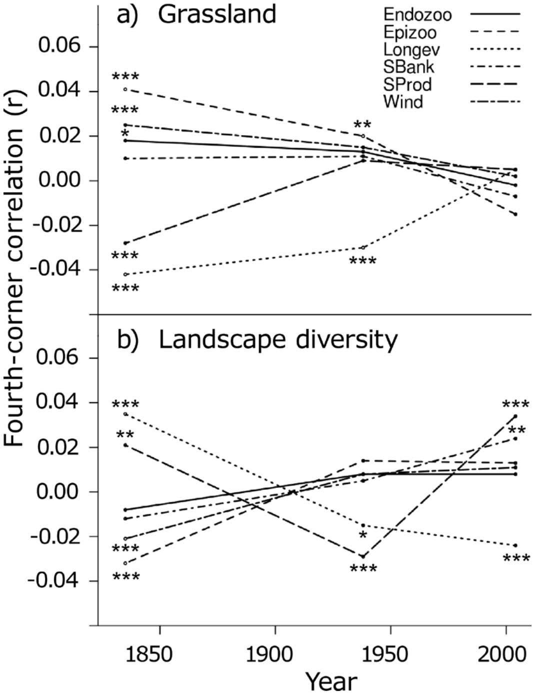

Fig. 2. Correlations between the six dispersal traits and a) percentage of grassland and b) diversity of the surrounding landscape at three time intervals: present-day (2004) and past (1835 & 1938). Significant relationships are indicated *** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

Seed production is another factor that limits dispersal (Primack & Miao 1992). In our study, species that produce low numbers of seed were mainly found in grassland sites that were surrounded by high amounts of grassland in the past, suggesting that colonization success of species with low seed production was higher in the historical landscape, and that these species are more strongly affected by landscape fragmentation than species that produce large numbers of seeds (Tilman 1994). The results in Paper II suggest that long-distance dispersal processes are no longer contributing to the colonization (dispersal and establishment) of grassland species within the increasingly fragmented landscape, and that local communities are increasingly becoming dominated by long-term persistent species.

Drivers of dispersal trait diversity

However, the loss of specific dispersal vector may be compensated for, if the species within a local community have a wide range of dispersal and persistence strategies (i.e. if a community has a high diversity of dispersal and persistence traits). In Paper III, we assessed the diversity of dispersal

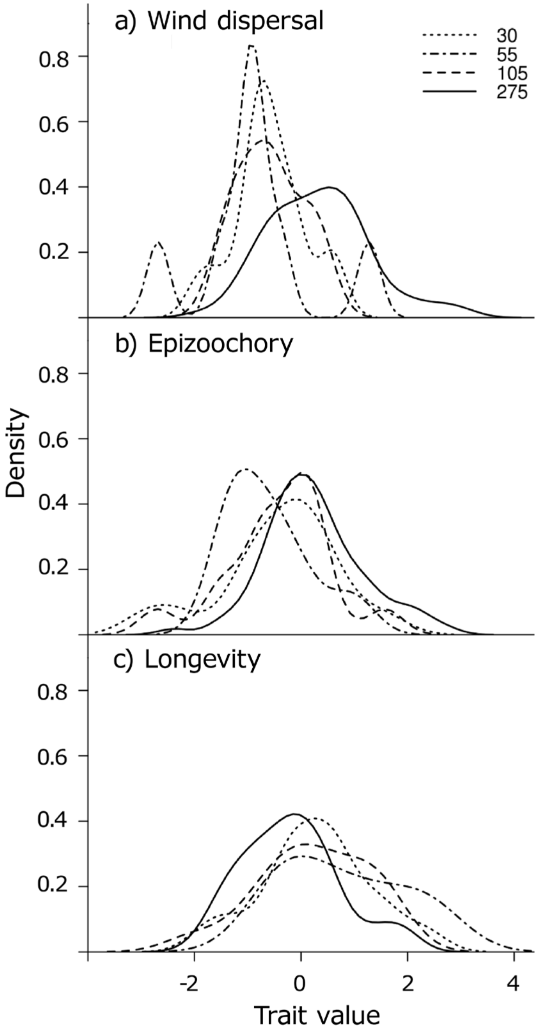

Fig. 3. Probability density plots showing the distribution of a) wind dispersal potential, b) epizoochory and c) adult plant longevity for different grassland age classes (30, 50, 105 and 275 years of grazing continuity). Mean trait values (at the grassland polygon level) were standardized with mean = 0, standard deviation = 1.

and persistence traits (multivariate range and dispersion of trait values) within grassland sites, and demonstrate that there were many sites which had a trait diversity that was higher or lower than expected from randomly generated communities (Fig. 1 in Paper III), indicating that there were underlying environmental filters that restrict the range and dispersion of dispersal and persistence trait values in these communities (Kembel 2009; Schamp & Aarssen 2009). Because plant colonization (dispersal and subsequent establishment) depends on dispersal between grassland patches and establishment in suitable microsites, gradients of landscape complexity and/or disturbance intensity are likely to have acted as filters that constrain the diversity of different trait values in the local communities.

Dispersal trait diversity (functional richness and functional divergence) was mainly determined by the history of a site and its surrounding landscape. Functional divergence, a measure of the extent to which species have different/distinct dispersal and persistence trait values, was highest in old grassland sites and in sites that were surrounded by large amounts of grassland habitat within the historical landscape. The structure of the historical landscape is likely to have facilitated dispersal by multiple vectors and long-term grazing continuity may have ensured the availability of suitable microsites (gaps) in which seeds can establish, once they have arrived there – generating communities that contain species with a wide range of different dispersal strategies.

Our results demonstrate that the long-term grazing continuity, and a high amount of dispersal sources in the surrounding landscape, not only enhances long-distance dispersal potential by single vectors (Figs. 2, 3), but also contribute to a higher diversity of different dispersal and persistence strategies within the present-day grassland sites.

Although current grazing management had no direct effect on trait diversity, we found that the effect of present-day grazing intensity on dispersal trait diversity depended on the structure of the landscape that surrounded the grassland sites in the past. Current grazing management promotes

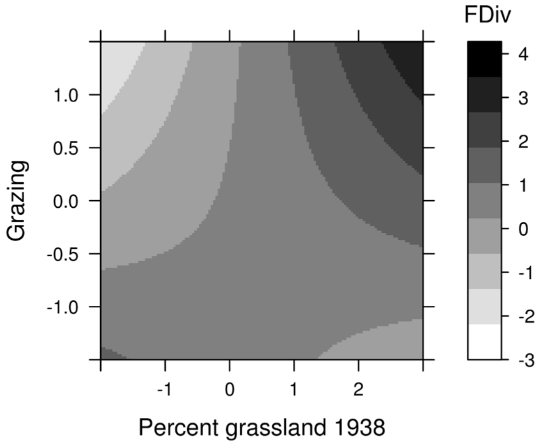

Fig. 4. Dispersal trait diversity (FDiv; light grey to black shading) in response to the interaction between present-day grazing intensity (Grazing) and amount of grassland in the historical landscape in 1938.

a higher diversity of dispersal and persistence traits within grasslands, but only if the sites were surrounded by large amounts of grassland habitat in the past (Fig. 4).

Functional richness of dispersal and persistence traits, a measure of the multivariate range of trait values within a community, was lower than expected from random communities in the youngest sites and sites that were overgrown by trees (Table 2 in Paper III). The low functional richness values in the young grasslands are a reflection of low proportions of long-distance dispersed species (Fig. 3 in Paper III), whereas high levels of shading and high amounts of litter in sites that are overgrown by trees appear to have selected for long-term persistent species (Fig. 3 in Paper III).

Temporal changes in biodiversity

An understanding of (a) how different facets of biodiversity change after ecosystem disturbance and (b) the processes that underlie (produce) these changes is crucial for more accurate predictions about how biodiversity and its associated functions will respond to future environmental changes (Noble & Gitay 1996; Loreau et al. 2003; Prach & Walker 2011).

In Paper V we assessed taxonomic, phylogenetic and functional (alpha and beta) diversity at four stages along a more than 300 year long chronosequence, representing an arable to semi-natural grassland succession. We then aimed to scrutinize which mechanisms might have been responsible for changes in these different facets of biodiversity.

Within-community (alpha) diversity

Although all three facets (taxonomic, phylogenetic and functional) of within-community (alpha) diversity increased during succession, they showed contrasting patterns of change over time (Fig. 5). Species richness increased steeply between early and early-mid succession (5-50 years), but the fact that there was no concurrent increase in phylogenetic or functional alpha diversity indicates that mainly closely related and functionally similar species enter the communities between the early and early-mid successional stages.

Null model analysis revealed that the functional diversity in early and early-mid successional communities was lower than expected given the observed levels of species richness (Fig. 6), suggesting that filtering effects have selected for species with specific sets of traits, which cause that these communities contain species that are functionally more similar than predicted by chance. Such filtering processes may provide an explanation of why there is no increase in functional diversity between the early and mid successional stages, despite the strong increases in species richness. The fact that the communities in early and mid succession mainly consist of wind dispersed species (Fig. 5 in Paper V), indicates that there is strong trait-based dispersal filtering,

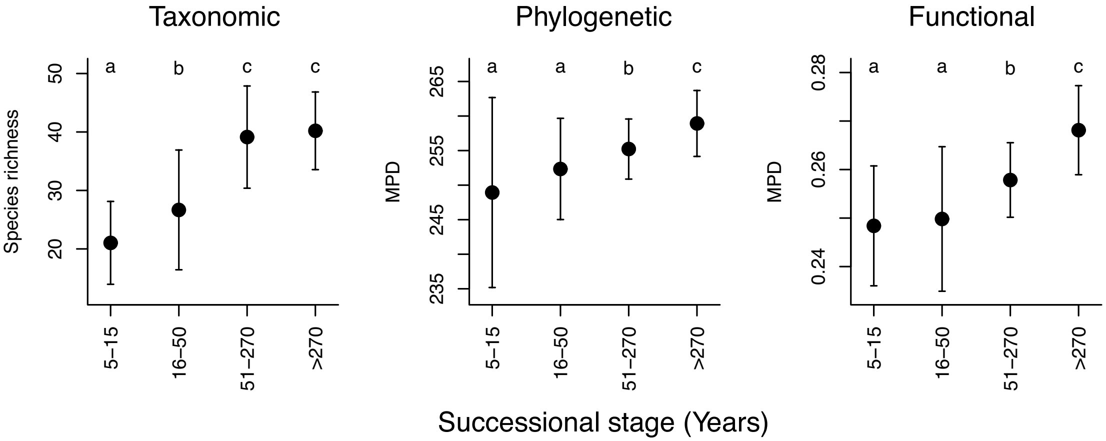

Fig. 5. Taxonomic, phylogenetic and functional alpha diversity (mean ± 1 SD) within four successional age classes. Phylogenetic and functional alpha diversity are represented by the mean pairwise distance (MPD). Letters indicate significant differences between the successional timesteps.

which favours species that have a high long-dispersal potential. We also found that early and early-mid successional communities mainly consisted of tall species that had a high seed production as well as high specific leaf area (SLA; Fig. 5 in Paper V). The effects of large scale disturbance and fertilization from former agricultural cultivation that are likely to have persisted in the early successional stages are likely have acted as filters that have selected for fast growing and stress-tolerant species (Fraterrigo et al. 2005; Carbajo et al. 2011).

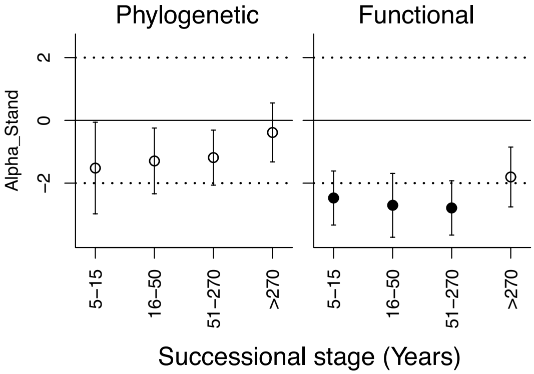

Fig. 6. Standardized effect sizes of phylogenetic and functional alpha diversity (mean ± 1 SD). Values < 0 indicate that phylogenetic or functional alpha diversity is lower than expected, given the species richness. The dotted lines indicate the 0.05 significance levels. Values < -2 (black dots below the lower dotted line) indicate that functional diversity is significantly lower than expected (functional clustering).

Although there was no change in phylogenetic and functional alpha diversity between early and early-mid succession, phylogenetic and functional diversity steeply increased between late-mid (50-270 years) and late succession (>270 years; Fig. 5). The lack of change in species richness, although phylogenetic and functional diversity increased, indicates that closely related and functionally similar species are replaced by phylogenetically and functionally more unique species between late-mid and late succession. The species within the late successional communities were functionally less similar than in the early successional communities (Fig. 6), suggesting that the relative importance of abiotic and trait-based dispersal filters has decreased over time and competitive exclusion of functionally similar species becomes more important in late succession where the vegetation sward is more dense and resources (e.g. Phosphorus; Fig. 6 in Paper V) become limiting.

Between-community (beta) diversity

While the taxonomic, phylogenetic and functional diversity within communities increased throughout succession, all three facets of beta diversity decreased (Fig. 3 in Paper V). Although communities become more diverse internally, they become taxonomically, phylogenetically and functionally more homogeneous during the course of succession.

Null model analysis revealed that throughout succession the decline of functional beta diversity was more rapid than expected from the temporal decrease in taxonomic beta diversity (Fig. 4, Paper V). Within all successional stages, communities tended to be phylogenetically as well functionally more dissimilar than expected, given the taxonomic beta diversity (Fig. 4, Paper V). As with the results from the analysis of functional alpha diversity (Fig. 6), functional beta diversity showed the strongest deviations from random expectations within the early and mid successional stages (Fig. 4, Paper V), suggesting that dispersal limitation and/or underlying environmental gradients determine the species turnover, with respect to their traits, in early and mid succession. Our finding that communities become more homogeneous in the late successional stages is likely to reflect (a) the lower levels of dispersal limitation in the old grasslands (Fig. 5, Paper V) and (b) the fact that grassland sites become more similar with respect to their environmental conditions as succession proceeds (Fig. 6, Paper V).

In contrast to the functional diversity, phylogenetic diversity did not differ significantly from random expectations in any of the successional stages (Fig. 4, Paper V). The non-congruent patterns in phylogenetic and functional alpha diversity suggest that there are low levels of trait conservatism, and that closely related species do not share similar traits. This interpretation is supported by the results of a test for phylogenetic signal which revealed low phylogenetic signal in each of the eleven traits that were used to calculate the functional diversity (Table A4 in Supplementary material of Paper V). In our study, phylogenetic similarity is a poor reflection of functional similarity and therefore has only limited ability to (a) detect community assembly processes and (b) predict changes in ecosystem functioning.

Conclusions

The results of the present thesis emphasize:
a) that multiple facets of biodiversity should be considered in order more realistically assess the full dimensions of the biodiversity loss resulting from human-driven environmental changes,
b) the importance of history as a major determinant of biodiversity, and
c) that the simultaneous consideration of multiple facets of biodiversity can provide new insights into the processes that shape communities.

The range of traits (i.e. functional trait diversity) within a community as well as the number of species that carry these traits influence the functions that an ecosystem is able to provide. The results of this thesis show that both grassland plant species richness and functional trait diversity in grassland sites were to a large extent explained by the land use history of the sites and the availability of grassland habitat in the surrounding historical landscape (Papers I & IV). Information on local management history as well as landscape history is likely to contribute to better predictions about the response of grassland biodiversity, and its associated functions, to future habitat destruction than can be obtained solely on the basis of descriptors of the current environment. It appears that not only is there a delayed loss of species diversity in response to landscape fragmentation (a phenomenon referred to as the "extinction debt") but that there is also a delayed decline of functional diversity in response to ongoing habitat destruction (i.e. a "functioning debt"; Gonzalez et al. 2009) that will potentially generate a time lag in the changes in ecosystem attributes.

The extent to which plant communities can track future environmental change will be determined by the ability of their component species to disperse and to persist. The results of the present thesis illustrate the importance of local management history as well as landscape history as determinants of both dispersal potential by single vectors and the diversity of different dispersal and persistence strategies within present-day grassland communities. Long-distance dispersal by wind and animals no longer appears to be contributing to the colonization of the remaining fragments of habitat within the increasingly fragmented modern landscape, and long-term persistent species are likely to dominate the grassland communities in the future. Long-term grazing continuity has promoted the diversity of dispersal and persistence traits within grassland communities. Whereas many long-distance dispersed species can still persist locally in the presence of disturbance which creates gaps that are available for establishment, grazing management may also promote the diversity of different dispersal and persistence strategies, but only in sites that were well connected to grassland areas in the past. The extent to which grassland management strategies can maintain a high diversity of dispersal and persistence strategies, and thereby the capacity of a plant community, and its associated functions, to buffer environmental change, will depend on the context of the site within the historical surrounding landscape.

The comparative analysis of taxonomic, phylogenetic and functional diversity at different stages of arable to semi-natural grassland succession provided insights into the temporal dynamics of the processes that drive biodiversity changes (Paper V). It is often debated to what extent community assembly after disturbance is random or deterministic. The results of this thesis demonstrated that the community assembly during secondary grassland succession was deterministic with respect to species traits, suggesting it may be possible to predict changes in biodiversity, and associated alterations in ecosystems functioning in future environments, on the basis of species functional traits. Trait-mediated environmental and dispersal filtering are likely to play a more dominant role in early and mid-succession, and the relative importance of competitive exclusion appears to increase in later successional stages. Taxonomic, phylogenetic and functional diversity show contrasting patterns of change over time. Short-term grazing management (5-50 years) promotes species richness, but does not enhance phylogenetic and functional diversity. However, only long-term grazing management, over more than 270 years promotes phylogenetic and functional diversity without further increases in species richness.

Overall, the results of this thesis suggest that the assessment of multiple facets of biodiversity and their linkages to current and historical environments is likely to contribute to a better understanding and more accurate predictions of biodiversity and ecosystem responses to future environmental change.

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I Grassland richness depends on scale and specialization

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Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialization

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Abstract

Questions: To what extent is species richness in semi-natural grasslands related to local environmental factors and (present/past) surrounding landscape structure? Do responses of species richness depend on degree of habitat specialization (specialists vs generalists) and/or scale of the study?

Location: Öland, Sweden.

Methods: Richness of herbaceous vascular plants (subdivided into richness of grassland specialists and generalists) was recorded within 50 × 50 cm plots and 0.1–4.8 ha grassland polygons. Generalized linear models and hierarchical partitioning were used to identify local factors (habitat area and heterogeneity, grazing intensity, habitat continuity) and landscape factors (proportion of surrounding grassland in 2004, 1938 and 1800, and landscape diversity in 2004) associated with the richness estimates.

Results: At the polygon scale, both specialist and generalist richness was positively associated with local habitat area and heterogeneity and, independently of area and heterogeneity, with grazing intensity, habitat continuity and amount of surrounding grassland in 1800. At the plot scale, specialist species richness was positively associated with habitat heterogeneity, amount of surrounding grassland in 2004 and landscape diversity. Plot-scale generalist richness was negatively associated with surrounding grassland in 1938 and positively associated with local grazing intensity.

Conclusions: Because both habitat specialization and study scale influence conclusions about relationships between species richness and local and landscape factors, the study highlights the need to consider species diversity at multiple spatial scales when making decisions about grassland management. Large-scale (polygon) species richness is influenced by immigration processes, with both specialists and generalists accumulating in old grasslands over centuries of grazing management. Habitat heterogeneity increased specialist species richness at both scales, suggesting that management policies should favour maintenance of a heterogeneous mosaic of open areas, trees and shrubs in temperate grazed grasslands. Although grassland specialists are sensitive to grassland isolation, in extensively managed landscapes with high landscape diversity input of grassland species from the landscape matrix may buffer negative effects of habitat fragmentation on grassland communities.

Introduction

Species that have restricted ecological preferences (habitat specialists) are likely to be more strongly affected by habitat loss and fragmentation than species that have broader ecological tolerances and are able to occupy a wider range of habitats (generalist species) (Polus et al. 2007; Devictor et al. 2008). For example, in Sweden, where there has

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been a 90% loss in the area of traditionally managed semi-natural grasslands since the beginning of the 20th century (Bernes 1994), and many of the plant species associated with semi-natural grasslands (grassland specialists) are included in the Swedish Red List of threatened and vulnerable species (Gärdenfors 2010). Grassland specialists can be defined as species that are dependent on, or favoured by, a long history of continuous grassland management by grazing and/or mowing (Ekstam & Forshed 1992). In addition to grassland specialists, semi-natural grassland communities also support many species that are as common or more common in other types of community – habitat generalists (Ekstam & Forshed 1992).

Concern about the loss of biodiversity – as a consequence of habitat fragmentation and the abandonment of traditional grassland management practices – has motivated an increasing interest in the mechanisms that influence grassland plant diversity (e.g. Bruun 2000; Krauss et al. 2004; Lindborg & Eriksson 2004; Adriaens et al. 2006; Helm et al. 2006; Gustavsson et al. 2007; Öster et al. 2007; Cousins & Eriksson 2008; Reitalu et al. 2009). Local environmental factors and structure of the surrounding landscape have been shown to both be significantly related to species diversity at different spatial scales in semi-natural grasslands (Adriaens et al. 2006; Öster et al. 2007; Pärtel et al. 2007; Cousins & Eriksson 2008; Reitalu et al. 2009). In addition to contemporary factors, management history and landscape history have also been shown to influence present-day grassland species diversity in semi-natural grasslands (Helm et al. 2006; Gustavsson et al. 2007; Reitalu et al. 2010). Studies investigating associations between levels of species richness, contemporary and/or historical habitat and landscape properties in semi-natural grasslands have typically focussed either on the total species richness (e.g. Lindborg & Eriksson 2004; Cousins et al. 2007; Öster et al. 2007) or richness within a suite of habitat specialist species – without considering the generalist species that co-occur in the same habitats (e.g. Bruun 2000; Gustavsson et al. 2007; Öster et al. 2007; Pärtel et al. 2007). However, studying species richness within species groups that differ in their degree of habitat specialization (specialists vs. generalists) may provide a more complete picture of the community-level consequences of habitat fragmentation than analyses focussing on total species richness or on the richness of specialist species alone (Adriaens et al. 2006; Polus et al. 2007; Brückmann et al. 2010).

Relationships between different local and landscape variables and species richness are expected to depend on the scale of the study (grain size) (Weiher & Howe 2003; Field et al. 2009). In studies of plant species richness in semi-natural grasslands, the scale of investigation varies from ≤ 1 m^2 (Öster et al. 2007; Aavik et al. 2008; Reitalu et al. 2009) to entire habitat patches (Bruun 2000; Krauss et al. 2004; Adriaens et al. 2006). The total species richness within grassland patches is often associated with the area of the patches and the within-patch environmental heterogeneity (Bruun 2000; Krauss et al. 2004; Adriaens et al. 2006; Cousins et al. 2007; Öster et al. 2007). Patch-level associations between species richness and the size and/or internal heterogeneity of the patches may potentially confound attempts to identify the contributions of other environmental or landscape variables to levels of within-patch richness. However, multivariate statistical methods, such as hierarchical partitioning (Chevan & Sutherland 1991), allow the influence of habitat area and/or heterogeneity to be partialled out before testing for the importance of other local and landscape factors.

Species richness in equally-sized samples, on the other hand, has been shown to be associated with different variables, depending on the study system: present and/or past habitat connectivity (Lindborg & Eriksson 2004; Pärtel et al. 2007), management regime (de Bello et al. 2006; Pärtel et al. 2007; Cousins & Eriksson 2008), management continuity (Aavik et al. 2008) and landscape context (Öster et al. 2007; Reitalu et al. 2009). European semi-natural grasslands are often characterized by exceptionally high levels of fine-scale vascular plant species richness (up to 60 species$\cdot$m^{-2} (Kull & Zobel 1991) and studies of semi-natural grasslands have often had a focus on fine-scale plant species richness or 'species density' (e.g. Kull & Zobel 1991; Öster et al. 2007; Aavik et al. 2008; Reitalu et al. 2009).

The present study focuses on vascular plant communities in semi-natural grasslands in a local agricultural landscape on the Baltic island of Öland, Sweden, and explores the relationships between species richness, at two spatial scales, and a series of factors describing local environment, habitat structure and history. We asked the following questions:

1. To what extent is plant species richness in semi-natural grasslands explained by local habitat characteristics (e.g. grassland area, environmental heterogeneity, management intensity and continuity)?
2. To what extent is plant species richness in semi-natural grasslands associated with the past and present properties of the surrounding landscape (e.g. landscape diversity and habitat connectivity)?
3. Do the responses of plant species richness to local and landscape factors depend on the degree of habitat specialization (specialists vs generalists) and/or the scale of the study?

Methods

Study area

The study area covers approximately 22.5 km^2 on the Baltic island of Öland, Sweden (centred on 56°40′49″ N, 16°

33′58″ E). At the beginning of the 19th century ca. 80% of the landscape was covered by grassland, but by 1938 the grassland area had decreased to 25% (Fig. 1). The present-day landscape is characterized by a mosaic of arable cultivation, deciduous forest and grasslands, and only 9% of the area remains as semi-natural grassland (Fig. 1). Land-use/vegetation maps (at a scale of 1:10 000) have been produced for the area for the time periods 1723–1733, 1792–1810, 1821–1851, 1938, 1959 and 1994/2004 using aerial photographs and historical maps (Johansson et al. 2008).

Vegetation sampling

In the present-day map of the study area in Johansson et al. (2008), the land cover was divided into ten categories: semi-natural grassland, alvar grassland, cultivated grassland, other grassland, arable land, closed forest, semi-open forest, hazel scrub, wetland and other land use. The 98 semi-natural grassland fragments in the study area were further subdivided and classified into grassland polygons on the basis of the historical continuity of grassland management, previous land use, present bush and tree cover, and the present-day moisture status (Fig. 1). The continuity/previous land-use classification was created using GIS overlay analysis of land-cover maps from different time periods (Prentice et al. 2007; Johansson et al. 2008). Bush and tree cover, and moisture status were classified using interpretations of near infrared aerial photographs from 1994 (updated with field validation in 1997 and 2004). As a result, a ‘grassland polygon’ can be defined as a spatially delimited area of semi-natural grassland, which belongs to a single continuity category and single type of previous land use, and that is relatively homogeneous in terms of bush cover, tree cover and moisture status. Vegetation was sampled from ‘old’ grassland polygons with long grassland continuity (>280 yr) as well as from polygons with grassland continuities of 30, 55 and 105 yrs on previously arable sites. A total of 113 grassland polygons with sizes varying between 0.1 and 4.8 ha (mean = 0.8 ha) (Fig. 1) were sampled at two nested spatial scales: the plot scale and the polygon scale. Early-successional grasslands, derived from nutrient-rich arable sites and with a grassland continuity of less than 30 yrs, were not included in the study.

The individual grassland polygons contained a fine-scale mosaic of dry and moist habitats, as well as areas of moderately eutrophicated vegetation (Prentice et al. 2007). In order to standardize the type of vegetation that was sampled, both within and among polygons, and to avoid the confounding effects of variation in soil moisture and nutrient levels, we restricted our vegetation sampling to dry semi-natural grassland vegetation, with low levels of eutrophication, by using the presence/absence of indicator species (cf. the bioassay approach of Prentice & Cramer 1990).

We first identified more-or-less uniform sampling areas that contained the grasses *Festuca ovina* and/or *Helictotrichon pratense* within each of the 113 grassland polygons. Both of these species are widespread in dry and mesic grasslands within the study area (Prentice et al. 2007), but avoid eutrophicated habitats (cf. Ellenberg et al. 1991; Ekstam & Forshed 1992). Vegetation patches where the cover of species regarded as indicators of eutrophication or moisture [including e.g. *Artemisia absinthium* and *Carex flacca* (cf. Bengtsson et al. 1988; Ellenberg et al. 1991)] exceeded 10% were excluded from the sampling area. An earlier study in the area (Reitalu et al. 2009) used the same standardized sampling approach, and validated the method by

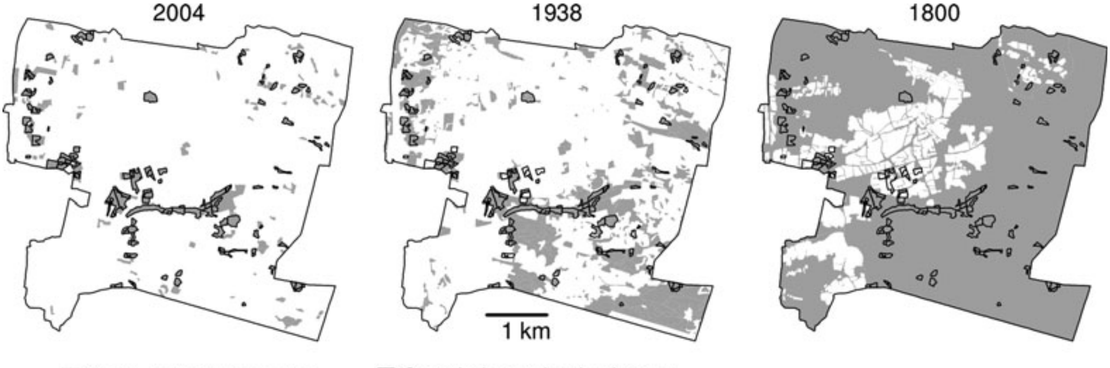

Fig. 1. Maps of the study area at three time periods: 2004, 1938 and 1800. The 113 grassland polygons which were sampled for vegetation in 2004 and in 2007 are marked on all three maps.

analysing soil samples from a random subset of the vegetation plots. Soil characteristics (water content, organic matter content, pH, total nitrogen and phosphorus contents, plant available phosphorus) showed little between-plot variation and there were no significant associations between the soil characteristics and fine-scale species richness.

For the plot-scale data, 50 × 50 cm plots were positioned randomly within the sampling areas, and the presence of all non-woody vascular plant species was recorded in the plots. The individual grassland polygons were represented by two to eight plots, with the numbers of plots being approximately proportional to the sizes of the polygons. A total of 425 plots were sampled in May–Jul 2004.

Polygon-scale richness data were collected from each of 113 grassland polygons, following the same rules as above for defining 'samplable' vegetation. Recording was carried out by extensively searching for vascular plant species in all the areas within a polygon that contained dry to mesic grassland vegetation – excluding eutrophicated areas, moist grasslands and areas with shrub or tree cover or other types of non-grassland vegetation. The time spent at each polygon (1–12 h) was adjusted to be proportional to the size of the polygon. The polygon-scale data were collected in May–Jul 2007.

Plant species that are characterized by Ekstam & Forshed (1992) as having their optimal occurrence in grasslands and pastures with long management continuity were defined as 'grassland specialists'; other species (those with no habitat preference or preferences for habitats other than grassland) were defined as 'generalist species' (Appendix S1). The species richness of each grassland polygon was characterized using four measures: (1) the plot-scale richness (averaged over the plots within the polygon) of grassland specialist species; and (2) generalist species; (3) the polygon-scale richness (total number of species found in the sampled areas within the polygon) of grassland specialist species; and (4) generalist species.

Local variables

Within-polygon habitat heterogeneity was characterized on the basis of estimates of seven different 'sub-habitats' within the polygons: cover of trees, cover of *Prunus spinosa*, cover of *Juniperus communis* and cover of *Corylus avellana*, and the proportions of tracks, moist areas and eutrophicated areas. The moisture status of the vegetation was assessed using a set of indicator species (e.g. *Carex flacca*, *Sesleria caerulea*, *Antennaria dioica*; cf. Bengtsson et al. 1988; Ekstam & Forshed 1992). The eutrophication status was assessed in terms of vegetation colour and lushness, and the presence of animal dung (cf. Prentice et al. 2007). Within-polygon habitat heterogeneity was calculated using the Shannon diversity index $H' = -\sum p_i * \ln p_i$, where p_i is the proportion of each sub-habitat within the polygon.

The total area (ha) was calculated for each polygon and log-transformed prior to the statistical analyses. The results of a GIS overlay analysis of land-cover maps from different time periods (Johansson et al. 2008) were used to assign the sampled grassland polygons to four continuity classes (defined as years-before-2004): >280, 105, 55 and 30 yrs.

The present-day management status of grassland polygons in the study area varies from well grazed to abandoned. Both grazed and abandoned grasslands were sampled, as long as the vegetation satisfied our sampling criteria. Grazing intensity was subjectively estimated (at a scale of 0–4) on the basis of vegetation height, the presence of grazing animals, signs of recent grazing and the presence of dung/droppings (cf. Reitalu et al. 2009).

Landscape variables

Landscape structure within a 300-m radius around grassland patches has been shown to have the strongest association with within-polygon species diversity in the same study area (Johansson 2008), and we therefore chose to use a 300-m radius buffer zone to characterize the landscape around each of the polygons in the present study. The proportion of grassland habitat in the 300-m buffer zone around each present-day grassland polygon was measured for each of three time periods: the present day (2004), 1938 and 1800. The diversity of the landscape matrix was estimated from the present-day map in Johansson et al. (2008), where the land cover was divided into ten categories: semi-natural grassland, alvar grassland, cultivated grassland, other grassland, arable land, closed forest, semi-open forest, hazel scrub, wetland and other land use. We estimated the proportions of these ten land-cover categories within the 300-m buffer zone surrounding each polygon and used the Shannon diversity index, based on these proportions, to characterize the diversity of the surrounding landscape.

Statistical analyses

The inter-correlations between the explanatory variables and the inter-correlations between the richness levels at different scales were tested using Pearson's product-moment correlation coefficients. Generalized linear models (GLMs) with a Poisson error distribution were used to examine associations between species richness (polygon-scale richness of specialists and generalists and plot-scale richness of specialists and generalists), the explanatory variables characterizing the grassland polygons (heterogeneity, area, age and grazing intensity) and the explanatory variables characterizing the surrounding landscape

(landscape diversity, proportions of grassland in 2004, in 1938 and in 1800). We checked for the possible effect of collinearity by calculating variance inflation factors for all four GLMs. Because all variance inflation factor values were below three, indicating no collinearity in the explanatory variables (see Zuur et al. 2007), we included all the variables in the analysis.

Hierarchical partitioning (Chevan & Sutherland 1991) was used to estimate the independent contributions of each of the explanatory variables in the multivariate GLMs. Randomization tests (based on 299 randomizations) were used to estimate the significances of the independent contributions of each of the explanatory variables. Hierarchical partitioning in combination with randomization tests allows the influence of habitat area and heterogeneity to be partialled out before testing for the significances of the independent contributions of the remaining explanatory variables.

Analysis of covariance was used to evaluate whether the slopes of the regression lines of specialist and generalist species richness were significantly different in relation to each of the explanatory variables (heterogeneity, area, age and grazing intensity, landscape diversity, proportion of grassland in 2004, in 1938 and in 1800).

All statistical analyses were carried out using the R programming environment (Version 2.10.1, R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org). The R package 'hier.part' (Hierarchical Partitioning. Version 1.0-3; http://www.R-project.org) was used for the hierarchical partitioning analysis.

Table 1. Summary of the species richness data at the polygon scale and at the plot scale.

	Mean ± SD Polygon Scale	Mean ± SD Plot Scale	Total Number of Species
Grassland Specialist Species	63 ± 11	21 ± 4	142
Generalist Species	40 ± 8	5 ± 3	143

Results

A total of 285 plant species was recorded within the 113 semi-natural grassland polygons (see Table 1 for summary data of species richness at different scales, and Appendix S1 for a complete species list). While the levels of plot-scale and polygon-scale specialist species richness were significantly correlated ($r = 0.39$, $P < 0.001$), the levels of generalist species richness at the two scales were not correlated ($r = 0.12$, $P = 0.21$). Total plot-scale richness was significantly but weakly correlated with total polygon-scale richness ($r = 0.23$, $P = 0.014$). The absolute values of correlation coefficients (r) between the explanatory variables did not exceed 0.43 (Table 2).

The GLM and hierarchical partitioning analyses showed that species richness variables at the polygon scale and at the plot scale were significantly associated with several local and landscape variables (Table 3, Fig. 2). At the polygon scale, the levels of species richness of both specialists and generalists increased significantly with polygon area and habitat heterogeneity (Table 3, Fig. 2). However, after accounting for the effects of polygon area and habitat heterogeneity, the effects of grassland continuity, grazing intensity and the proportion of grassland in 1800 contributed significantly ($P < 0.05$) to the explanation of variation in species richness of both grassland specialists and generalists (Fig. 2). At the polygon scale, species richness of grassland specialists and generalists showed similar relationships with the explanatory variables: both were positively associated with polygon area, habitat heterogeneity, grazing intensity, grassland continuity and with the proportion of grassland in 1800 (Table 3). The analysis of covariance showed no significant differences between the levels of species richness of specialists and generalists in relation to the tested explanatory variables at the polygon scale.

At the plot scale, the levels of species richness of grassland specialists and generalists differed in their relationships with several explanatory variables. The largest

Table 2. Inter-correlations between explanatory variables ($N = 113$).

	log (Area)	Continuity	Grazing Intensity	Landscape Diversity	Grassland 2004	Grassland 1938	Grassland 1800
Habitat Heterogeneity	0.38 ***	0.21 **	0.29 ***	0.21 *	+	+	+
log(Area)		0.15 *	0.15 *	+	0.16†	+	–
Continuity			–	–	–	–	+
Grazing Intensity				0.24 ***	0.13†	0.17 *	–
Landscape Diversity					+	0.36 ***	+
Grassland 2004						0.27 **	–0.30 **
Grassland 1938							0.43 ***

The significances of the Pearson's product moment correlations are indicated.
***$P < 0.001$, **$0.001 < P < 0.01$, *$0.01 < P < 0.05$, †$0.05 < P < 0.1$). For variables with $P \geq 0.1$, only the sign of the correlation coefficient is given.

Table 3. Results from generalized linear models (GLM) explaining species richness of specialists and generalists at the polygon and plot scales.

	Polygon-Scale Richness			Plot-Scale Richness		
	Specialists	Generalists	*P* diff.	Specialists	Generalists	*P* diff.
Local Variables						
Habitat Heterogeneity	+ **	+		+ *	–	***
log (Area)	+ ***	+ ***		+	–	–†
Continuity	+†	+†		+	–	
Grazing Intensity	+ **	+ ***		+	+ **	
Landscape Variables						
Landscape Diversity	+	+		+ *	+	
Grassland 2004	+	–		+ *	–	**
Grassland 1938	–	+		–	– *	*
Grassland 1800	+ **	+ *		–	+†	

The full model, including all local variables (characterizing grassland polygons) and landscape variables (characterizing the landscape within a 300-m radius around the grassland polygons), is presented.

***$P < 0.001$, **$0.001 < P < 0.01$, *$0.01 < P < 0.05$, †$0.05 < P < 0.1$). Only the sign of the association is given for variables with $P \geq 0.1$. The significance of the comparisons of the slopes of the regression lines (chi-square tests) for specialist and generalist species richness is given by '*P* diff'.

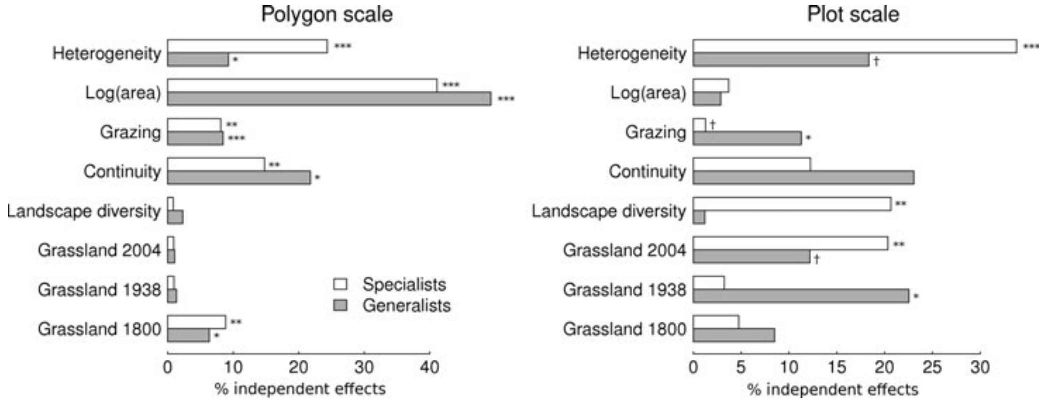

Fig. 2. Results from the hierarchical partitioning, explaining the species richness of specialists and generalists at the scales of polygons and plots. The significances of the independent contributions of each of the explanatory variables are indicated (***$P < 0.001$, **$0.001 < P < 0.01$, *$0.01 < P < 0.05$, †$0.05 < P < 0.1$).

significant ($P < 0.05$) proportion of the variation in grassland specialist species richness was explained by the positive association with habitat heterogeneity, followed by positive associations with landscape diversity and with the proportion of surrounding grassland in 2004 (Fig. 2, Table 3). The largest significant contributions to the explained variation in the plot-scale richness of generalist species, on the other hand, were from the negative association with the proportion of surrounding grassland in 1938 and the positive association with grazing intensity (Fig. 2, Table 3). The analysis of covariance showed that the levels of species richness of specialists and generalists differed significantly ($P < 0.05$) in relation to habitat heterogeneity, polygon area, landscape diversity and the proportion of grassland within a 300-m radius in 2004 (Table 3).

Discussion

Both local habitat characteristics (area, environmental heterogeneity, continuity and grazing intensity) and properties of the surrounding landscape (landscape diversity, present and past grassland connectivity) were associated with species richness in semi-natural grasslands. The responses of plant species richness to local and landscape factors depended on the degree of habitat specialization (grassland specialists vs generalists) and the scale of the study (polygon scale vs plot scale). Our results suggest that, whereas the richness of both specialists and generalists at the polygon scale are influenced by similar processes, the plot-scale richness of specialists and generalists are responding to different processes.

The definition of specialist and generalist species might be expected to have influenced, at least to some degree, the results of the study. We chose to follow the classification of Ekstam & Forshed (1992), where species that have their ecological optima in grasslands and pastures with long management continuity are defined as 'grassland specialists'. Other studies of Swedish semi-natural grasslands (e.g. Gustavsson et al. 2007; Öster et al. 2007) have used a more restricted definition of specialist species, combining a species' sensitivity to reduced grazing intensity with a management continuity criterion. We tested the sensitivity of our results to differences in the definition of specialist species by repeating our analyses with richness levels calculated using the stricter definition of specialist species (Gustavsson et al. 2007; Öster et al. 2007). The results obtained using the two definitions were similar, suggesting that the associations with environmental and landscape variables, and the overall conclusions in the present study, are likely to be relatively robust with respect to slight differences in the classification of species into specialist and generalist categories.

Polygon-scale richness

Local habitat characteristics (grassland continuity and grazing intensity) explained a greater proportion of the variation in polygon-scale species richness than factors related to the surrounding landscape structure – even after accounting for the effects of grassland area and heterogeneity.

The amount of grassland in the surrounding landscape in 1800 was the only landscape factor that was significantly associated with polygon-scale species richness of both grassland specialists and generalists. Significant associations between present-day species richness and past landscape structure are often interpreted in terms of an extinction debt, which reflects a slow population response to habitat fragmentation (Lindborg & Eriksson 2004; Helm et al. 2006). In the present study, the fact that both old and young grasslands were included in the analyses means that the associations between present-day species richness and the proportion of the surrounding grassland in 1800 do not reflect a simple extinction debt. The formation of typical species-rich grassland flora on abandoned arable fields depends on the vicinity of old grassland areas for seed sources (Cousins & Aggemyr 2008). The positive association between the proportion of grassland in 1800 and present-day species richness of grassland specialists and generalists suggests that the formation and persistence of a species-rich grassland flora is facilitated in areas that are, or have historically been, surrounded by old grasslands (cf. Reitalu et al. 2009).

In addition to the historical landscape structure, the continuity of the local grassland polygons was (independently of polygon area and heterogeneity) associated with present-day species richness of both grassland specialists and generalists at the polygon scale. Land-use effects have been shown to influence soil conditions for more than 80 yrs after the abandonment of agriculture (Falkengren-Grerup et al. 2006), and the effect of habitat continuity on species richness may therefore potentially be confounded with the effects of differences in soil conditions. In the present study, the vegetation sampling strategy was standardized to avoid major differences in soil moisture and eutrophication within and between polygons. In addition, we used plot-scale soil data from an earlier study in the same area (Reitalu et al. 2009) that were available for a subset (49) of the polygons in the present study to test for differences in edaphic conditions in the four continuity categories. The results from a series of one-way ANOVAs revealed no significant associations between soil characteristics (water content, organic matter content, total nitrogen, total phosphorus and plant available phosphorus) and the continuity classes – suggesting that the associations between habitat continuity and species richness can be interpreted as being independent from differences in the soil conditions. As in previous studies (Honnay et al. 1999; Pärtel & Zobel 1999; Gustavsson et al. 2007), grassland continuity was positively associated with the polygon-scale richness of grassland specialist species in the present study. However, the richness of generalist species also increased with habitat continuity, suggesting that polygon-scale richness is influenced by immigration processes, and that both grassland specialist species and generalist species have accumulated in the old grassland polygons over centuries of grassland management. Eriksson et al. (2006) showed in an *in situ* experimental study that high species richness was no barrier to the establishment of new species in semi-natural grasslands in Sweden. In contrast, other experimental studies have shown that high species richness and, especially, high functional diversity hinder the entry of new species into grassland communities (Lanta & Lepš 2008; Petermann et al. 2010). All these invasion experiments were conducted at relatively small scales (0.25–4.00 m^2) and are therefore not directly comparable with our polygon-scale data. At the scale of the whole grassland polygons, both specialist and generalist species are likely to have a higher probability of finding a favourable window for establishment (both in time and space) if a polygon has had a long history of grassland management.

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A species–area relationship – a positive association between species richness and habitat area – is often revealed in grassland studies (e.g. Bruun 2000; Krauss et al. 2004; Adriaens et al. 2006; Cousins et al. 2007; Öster et al. 2007). In the present study, the polygon-scale richness of both specialist and generalist species was strongly positively associated with polygon area. In addition to habitat area, environmental heterogeneity within habitat patches has been shown to have a positive effect on plant species richness in several studies of forest and grassland communities (Honnay et al. 1999; Bruun 2000; Söderström et al. 2001; Öster et al. 2007). In the present study, habitat heterogeneity was (independently of habitat area) positively associated with the species richness of grassland specialists within polygons. Historically, grazed grasslands in Sweden, especially the common pasture areas outside villages (out-fields), were characterized as having a mosaic of trees, shrubs and open areas (Lindbladh 1999; Eriksson et al. 2002). The typical flora of old grasslands and pastures – the flora of grassland specialists – includes species with a variety of different sub-habitat preferences in relation to openness, disturbance, moisture and eutrophication (Ekstam & Forshed 1992).

In agreement with previous studies that have shown significant associations between management intensity and species richness in semi-natural grasslands (de Bello et al. 2006; Aavik et al. 2008), the polygon-scale richness of specialist species was significantly positively associated with grazing intensity. However, the richness of generalist species showed an even stronger positive association with grazing intensity. The higher richness of generalist species in the well-grazed grasslands is explained by the presence of annual species (e.g. *Erodium cicutarium* and *Geranium molle*) (Appendix S1), which occur in areas that have been disturbed by grazing animals. Our results suggest that the temporary or permanent abandonment of grazing management in grazed semi-natural grasslands is likely to be accompanied by a patch-scale decrease in species richness of both grassland specialists and generalists (cf. Reitalu et al. 2010).

Plot-scale richness

While polygon-scale richness was mainly influenced by local habitat characteristics, plot-scale richness was influenced by both local factors and properties of the surrounding landscape. In contrast to the polygon-scale richness, where specialists and generalists were similarly influenced by different explanatory factors, the levels of plot-scale species richness were associated with different environmental and landscape factors in the two groups of species.

The most important local habitat factors influencing plot-scale species richness were within-polygon habitat heterogeneity and grazing intensity. As at the polygon scale, the plot-scale richness of grassland specialists was positively associated with environmental heterogeneity within the polygons. The large actual species pool [species present in the community being investigated (Pärtel et al. 1996)] of specialist species in grassland polygons that contain high levels of habitat heterogeneity is likely to also have a positive influence on the plot-scale species richness (cf. Öster et al. 2007). In contrast to non-anthropogenic communities, environmental heterogeneity in semi-natural grasslands may be strongly influenced by management decisions of farmers. Our results suggest that the wholesale removal of trees and shrubs from grazed grasslands is likely to have a negative effect on species richness of grassland specialist species, both at the scale of whole grassland patches and at a fine scale.

Fine-scale generalist species richness, on the other hand, was not related to habitat heterogeneity but was positively associated with grazing intensity, with annual species being favoured by grazing and fine-scale disturbances (cf. Appendix S1).

While polygon-scale species richness was associated with grassland history, the plot-scale richness of grassland specialists was mainly associated with the descriptors of present-day landscape structure. Whereas polygon-scale species richness is strongly influenced by the occurrence of less common species within the grassland polygons (cf. Magurran 2004), fine-scale species richness is likely to reflect species abundance patterns within grassland patches/polygons – with species that have high abundances having a higher probability of occurring in the sampling plots. If a grassland polygon is characterized by a high fine-scale (within-plot) richness of grassland specialists, it can be expected that the specialist species also occur in relatively high abundances in the polygon. The proportion of grassland area within a 300-m radius around the polygons in the present landscape was positively associated with the plot-scale richness of specialists – indicating that the abundances of grassland specialists are higher in polygons that are surrounded by other grassland areas and lower in polygons that are isolated (surrounded by forest or arable fields). Average abundance of grassland specialists (estimated as the average proportion of plots occupied by specialist species within each polygon) was, indeed, significantly positively correlated with proportion of surrounding grassland in 2004 ($r = 0.28$, $P = 0.003$). The fine-scale richness of generalist species, on the other hand, was negatively associated with the proportion of surrounding grassland in 1938. High amounts of non-grassland habitat in the surrounding landscape may have contributed to the immigration of generalist species (cf. Kiviniemi & Eriksson 2002) – leading to an increased abundance of generalists in the grasslands that have been isolated since 1938.

Studies of insect communities (e.g. Krauss et al. 2003; Batáry et al. 2007) have shown that high landscape diversity in the surrounding areas has a positive effect on generalist species richness within grassland habitat patches. Our results show that, while the richness of generalist species was negatively associated with surrounding grassland area, it was not significantly associated with landscape diversity. In contrast, there was a positive association between the richness of grassland specialists and landscape diversity. Our study area is located in a relatively extensively managed landscape (Forslund 2001), and the landscape matrix includes habitat types (road verges, alvar grasslands, recently abandoned arable fields, cultivated grasslands, semi-open forests; Johansson et al. 2008) that also provide pockets of suitable habitats for a number of grassland specialist species. While the richness of generalists benefits from grassland isolation (regardless of the surrounding habitat types), the richness of grassland specialists is negatively influenced by grassland isolation. However, a highly diverse landscape surrounding fragmented grassland patches may decrease the negative influence of habitat isolation by improving the functional connectivity for grassland specialist species (cf. Cousins 2006; Öckinger & Smith 2008). The negative effects of habitat fragmentation on grassland communities in our study area (and probably also in other landscapes with a low intensity of management) are, therefore, likely to be buffered by the input of grassland species from a high-quality landscape matrix.

Conclusions

The present study showed that the richness of both specialists and generalist species was highest in old, well-grazed, heterogeneous grassland patches. Our results support the suggestion (Söderström et al. 2001) that management policies for temperate grasslands should favour the maintenance of a mosaic of open areas, trees and shrubs. Whereas richness of grassland specialist species was negatively influenced by grassland fragmentation, our results also suggest that, in extensively managed landscapes with high landscape diversity, an input of grassland species from the landscape matrix may buffer the negative effects of habitat fragmentation on grassland communities. Because habitat specialization and the scale of study are shown to influence conclusions about relationships between species richness and local and landscape factors in semi-natural grasslands, the study highlights the importance of considering species diversity at multiple spatial scales when making decisions about grassland management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of recorded species (taxa). The habitat preference (grassland specialist‘s’ or generalist‘g’), lifespan (annual‘a’, biennial‘b’ or perennial‘p’) and frequency of occurrence (%) in polygons (% pol) and in plots (% pl) is given for each species. Nomenclature follows Mossberg & Stenberg (2003).

II Linking landscape history and dispersal traits

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COMMUNITY ECOLOGY - METHODS PAPER

Linking landscape history and dispersal traits in grassland plant communities

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Abstract Dispersal limitation and long-term persistence are known to delay plant species' responses to habitat fragmentation, but it is still unclear to what extent landscape history may explain the distribution of dispersal traits in present-day plant communities. We used quantitative data on long-distance seed dispersal potential by wind and grazing cattle (epi- and endozoochory), and on persistence (adult plant longevity and seed bank persistence) to quantify the linkages between dispersal and persistence traits in grassland plant communities and current and past landscape configurations. The long-distance dispersal potential of present-day communities was positively associated with the amounts of grassland in the historical (1835, 1938) landscape, and with a long continuity of grazing management—but was not associated with the properties of the current landscape. The study emphasises the role of history as a determinant of the dispersal potential of present-day grassland plant communities. The importance of long-distance dispersal processes has declined in the increasingly fragmented modern landscape, and long-term persistent species are expected to play a more dominant role in grassland communities in the future. However, even within highly fragmented landscapes, long-distance dispersed species may persist locally—delaying the repayment of the extinction debt.

Keywords Life-history traits · Persistence · Fourth-corner · Habitat fragmentation · Land-use history

Introduction

Dispersal is one of the key processes that allow plant species to track environmental change in space and time (Cain et al. 2000; Thomas et al. 2004; Nathan 2006). The degree to which species' distributions are dispersal-limited at different scales will be jointly determined by the species' dispersal traits and the spatial configuration of suitable habitat (Bullock et al. 2002; Poschlod et al. 2005; Ozinga et al. 2009). At the landscape scale, dispersal success will not only depend on species' ability to disperse but also on the distances between patches of suitable habitat and the configuration of the surrounding landscape (Eriksson et al. 2002). At the local scale, seed dispersal has been shown to play a major role in the colonization of available microsites (Grubb 1977; Bullock et al. 1995). In rapidly changing landscapes, plant species' distributional patterns often show a delayed response to habitat fragmentation (Peterken and Game 1984; Helm et al. 2006). While the spread of species between sites, and the subsequent establishment in

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suitable microsites within sites, may be increasingly limited by dispersal in space, species may still persist within sites for long periods of time under non-optimal conditions (extinction debt). The species composition and the distribution of dispersal and persistence traits in present-day plant communities may therefore be expected to reflect both the proximity of dispersal sources in the surrounding historical landscape and the long-term availability of regeneration niches (gaps) within sites (e.g., Rusch and Fernández-Palacios 1995; de Blois et al. 2001). Quantifying the relationships between species' dispersal and persistence traits and the historical characteristics of both landscape structure and the local availability of microsites for establishment will allow more realistic predictions about the future responses of species with specific sets of dispersal and persistence traits to ongoing landscape fragmentation and changes in local management regime (e.g., Johnson 1988; Lavorel and Garnier 2002).

No linkages between dispersal traits in present-day plant communities and historical landscape configurations have been detected in earlier studies (e.g., Hérault and Honnay 2005; Adriaens et al. 2006; Lindborg 2007). However, earlier studies have not attempted to link species dispersal traits directly to landscape characteristics using simultaneous analysis of matrices of species occurrence data, trait data and data on the historical descriptors. Instead, they have focussed on relationships between mean trait values (at the site level) or groups of functionally similar species, and the site or landscape descriptors. In addition, earlier analyses of relationships between dispersal traits and historical landscape characteristics have been based on the assignment of a single dispersal mode to an individual species, instead of viewing dispersal in terms of "dispersal potential" on a continuous scale and allowing for multi-vector dispersal (Poschlod et al. 2005).

The present study explores the ways in which current and past landscape configurations as well as local management history and current management status may explain the species composition, and the distribution of dispersal and persistence traits in semi-natural grassland plant communities. Semi-natural grasslands are among the most diverse plant communities within the European agricultural landscape, and long-distance seed dispersal by domestic animals and wind is known to be of central importance for plant colonization in these habitats (Fischer et al. 1996; Tackenberg et al. 2003). Landscape fragmentation and isolation, resulting from changes in management practices over the last centuries, are expected to decrease rates of long-distance dispersal and (re-)colonization of suitable habitats.

The first objective of our study was to quantify the relative importance of the historical and current characteristics of the landscape and local management regime as determinants of variation in plant community composition. To what extent are present-day plant communities dispersal limited at the local and landscape scales? The second objective was to quantify and test the linkages between species' dispersal and persistence traits, and the properties of the past and present landscape—taking into account community composition and using quantitative information on seed dispersal potential and persistence derived from recent trait databases (Poschlod et al. 2003; Kleyer et al. 2008). To what extent is the current distribution of dispersal traits in plant communities explained by the historical properties of the landscape?

Materials and methods

Study area

The Jordtorp area (56°33′58″N, 16°33′58E) is located on the Baltic Island of Öland (Sweden) and covers an area of 4.5 × 4.5 km with an overall flat topography (Prentice et al. 2006; Johansson et al. 2008; Reitalu et al. 2008). The present landscape is characterized by a mosaic of arable fields, deciduous forest and grasslands. Most of the forest has a semi-open character and contains many typical grassland plant species in the ground flora (Reitalu et al. 2008). The proportion of semi-natural grassland in the landscape has declined progressively since the early eighteenth century, from 86% in 1723 to 9% in 1994 (Johansson et al. 2008). Initially, grassland was lost to arable cultivation but, since the 1930s, grasslands have been lost to the forest encroachment that has followed the decline of traditional, extensive, grazing management.

Vegetation sampling

We recorded the presence/absence of semi-natural grassland plant species, between May and August 2007, in 113 grassland polygons that were classified according to their age (grassland continuity), previous land use (arable fields or old grasslands) and the characteristics of the present-day vegetation (bush and tree cover, and moisture status) by Johansson et al. (2008). Each grassland polygon represents a spatially delimited area of semi-natural grassland, that belongs to a single continuity category and single type of previous land-use, and that is relatively homogeneous in terms of bush cover, tree cover and moisture status. In order to avoid major gradients of edaphic variation, the vegetation sampling was restricted to dry grassland vegetation with low levels of eutrophication (cf. Reitalu et al. 2009). Within each polygon, we carried out an exhaustive search for all herbaceous, vascular plant species (186 species in total) within vegetation containing the grasses

Festuca ovina and/or *Helictotrichon pratense*. Both these species are widespread in dry and mesic grasslands within the study area and avoid eutrophicated habitats (Prentice et al. 2007). In order to reduce edge effects (see Reitalu et al. 2008), we did not sample the area within a 2-m-wide internal buffer zone along polygon borders. Sampling time per polygon ranged between 1–12 h and was proportional to the polygon area.

Local habitat descriptors (LOCAL)

At the grassland polygon scale (local scale), we subjectively estimated grazing intensity (Grazing) on a scale of 0–4 (ungrazed to well-grazed) on the basis of vegetation height, the presence of grazing animals and recent signs of grazing such as dung/droppings and cropped vegetation (Reitalu et al. 2008). The cover of trees (Tree_cov, in %) was used as a descriptor of light-availability (shading) and litter accumulation (Reitalu et al. 2008). Each grassland polygon was assigned to one of four age classes (Age): 30, 55, 105 and 275 years, defined as years of grassland continuity before 2004, using GIS overlay analysis of land-cover/vegetation maps produced from historical maps or aerial photographs (Johansson et al. 2008). The degree of habitat heterogeneity (Hab_div) was quantified by the Shannon–Wiener index estimated on the basis of the proportions (%) of seven different sub-habitats: the cover of trees, the cover of each of the shrub species *Prunus spinosa, Juniperus communis* and *Corylus avellana*, and the proportions of moist areas, eutrophicated areas and tracks. The total area (Area; in ha) of each grassland polygon was estimated by Johansson et al. (2008).

Landscape descriptors (LANDSCAPE)

Land-cover maps from three time periods, 1835, 1938 and 2004, were used to quantify the past and present landscape structure within a 300-m buffer zone surrounding the edges of each of the studied grassland polygons (Johansson et al. 2008). The choice of the buffer radius was based on the results of Johansson (2008), who tested the effect of different threshold radii on species diversity, and showed that landscape structure within a 300 m radius around grassland patches showed the strongest associations with within-polygon species richness. Two different landscape descriptors were used: (1) the percentage of grassland habitat (Grass_1835, Grass_1938, Grass_2004) and (2) the diversity of the landscape matrix (Land_div_1835, Land_div_1938, Land_div_2004), characterized using the Shannon–Wiener index, and ten habitat types: semi-natural grassland, alvar grassland, cultivated grassland, other grassland, arable land, closed forest, semi-open forest, hazel scrub, wetland and other land use (classified by Johansson et al. 2008).

Spatial descriptors (SPACE)

We generated a set of multi-scale spatial descriptors using the PCNM (principal coordinates of neighbor matrices) framework. In contrast to traditional spatial descriptors, such as the *x*- and *y*-coordinates and their polynomial terms, PCNM variables are independent of (orthogonal to) each other, and allow the modeling of more complex spatial patterns. We constructed PCNM variables following the (four-step) approach proposed by Borcard and Legendre (2002): (1) the *x*-*y* coordinates of the polygon centroids of the 113 sites were used to construct a Euclidean distance matrix; (2) the longest link (ca. 1,200 m) in the minimum spanning tree of the sites was chosen as a threshold distance; (3) the Euclidean distance matrix was truncated by substituting all distances exceeding the threshold distance by a value equalling four times the threshold distance—retaining only the distance values for closely connected sites; and (4) principal coordinates analysis was used to decompose the truncated distance matrix into eigenvectors. The 57 eigenvectors (PCNMs) that corresponded to positive eigenvalues represent spatial autocorrelation at scales between 1.2 km (PCNM 57) and 5.5 km (PCNM 1), and were included as spatial variables in the subsequent analyses of community composition.

Species' dispersal and persistence traits

We compiled a set of seven species-specific life-history traits, related to seed dispersal by different vectors and to persistence.

Two simple descriptive seed traits, the number of seeds per ramet (SProd) and the seed mass (SMass), were extracted from databases (Poschlod et al. 2003; Kleyer et al. 2008). We calculated mean trait values for species represented by multiple entries in the databases. Given the large variability in seed production in response to variation in abiotic conditions, we calculated the mean of the seed number per ramet, omitting 20% of the lowest and highest values.

Wind dispersal potential (Wind) on an ordinal scale ranging from 0 (low) to 7 (high) was extracted from information on the terminal velocity and release-height of the seeds (Poschlod et al. 2003) of 145 species, following the classification developed by Tackenberg et al. (2003). Cattle are the main type of grazing livestock within the study area, and we used the seed retention potential on cattle coats (defined as the percentage of seeds remaining attached to cattle coat after mechanical shaking for 1 h) as an indicator trait for epizoochorous dispersal potential (Epizoo). Data for 58 species were obtained from Römermann et al. (2005). Retention potential was predicted from seed mass and seed morphology for 107 additional species using the regression model proposed by Römermann et al. (2005). Endozoochorous dispersal potential (Endozoo) was estimated as the number of germinated seeds, corrected by the seed production per unit area according to the approach of Bruun and Poschlod (2006). Data on the number of germinated seed from cattle dung samples and estimates of species abundance (four classes on a logarithmic scale) in the grazed vegetation were obtained for 53 species from the studies by Bruun and Poschlod (2006) and P. Poschlod (unpublished data). Seed production per unit area was estimated as the product of log-transformed seed production per ramet (SProd) and the estimated abundance class. An endozoochory index was then calculated as the residuals of germinated seed regressed on seed output per unit area using model II regression of ordinary least squares (Legendre and Legendre 1998). The index is positive for species with higher seed numbers in the dung than expected from seed production alone, and negative for lower than expected numbers.

Adult plant longevity (Longev) was inferred for 182 species, from data on life span and clonal propagation available from databases (Poschlod et al. 2003; Kleyer et al. 2008) and data from P. Poschlod (unpublished data), using the following three classes: annual and biennial plants, perennial plants without the ability to spread clonally, and perennial plants showing clonality. The ability of species to build up a persistent soil seed bank was characterized by the longevity index (SBank) of Bekker et al. (1998) which represents the proportion of non-transient seed bank records in the database of Thompson et al. (1997)—calculated for the 117 species that were present with at least 5 observations in the database.

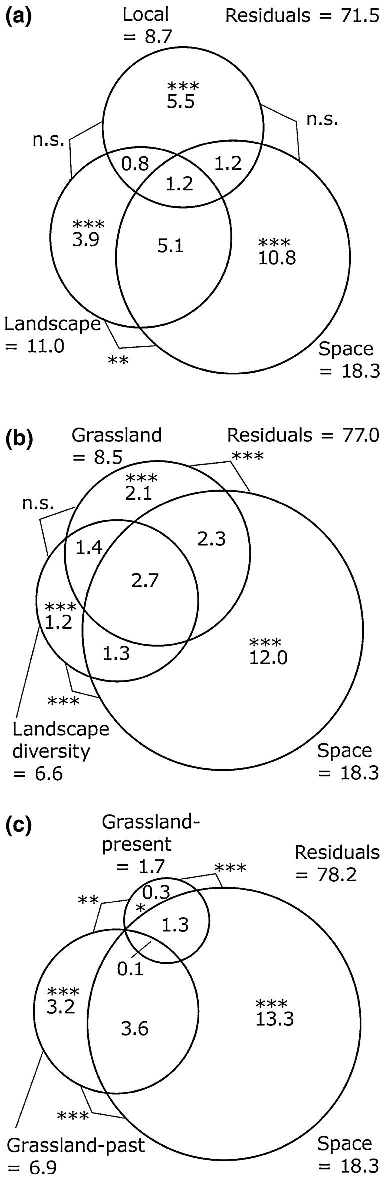
Statistical analysis

Community composition was analysed using redundancy analysis (RDA). We ran a forward selection procedure to identify the most parsimonious model for each of the three sets of explanatory variables, LOCAL, LANDSCAPE and SPACE, separately, following the approach of Blanchet et al. (2008). There was a significant, linear, spatial gradient in the response data. We therefore detrended the community matrix (using the geographic *x*–*y* coordinates as co-variates) prior to forward selection of the PCNM-variables, because many small- as well as large-scale spatial descriptors (PCNMs) would be needed to model simple, linear, spatial structures, leaving fewer PCNMs available for modeling spatial structures at smaller scales (Borcard and Legendre 2002).

Fig. 1 Variation partitioning showing the unique and shared contributions of the predictor sets (Local, Landscape, Space) to the explanation of variation in community composition. **a** *Local*, *Landscape* and *Space*; **b** the Landscape component from (**a**) decomposed into the amount of grassland (*Grassland*), diversity of surrounding landscape (*Landscape diversity*) and spatial structure (*Space*); **c** Grassland component from (**b**) decomposed into the amount of grassland in the present-day (*Grassland-present*) and historical (*Grassland-past*) landscapes and spatial fraction (*Space*). The numbers represent the sizes of the unique and shared contributions (R^2adj, in %). The significance of the unique fractions was tested using permutation tests. Differences between two unique contributions were tested for significance using the bootstrap test for fractions ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; *n.s.* non-significant ▶

In order to quantify the common and unique contributions of the three sets of variables (LOCAL, LANDSCAPE and SPACE), and subsets of these variables, to the total variation in the community matrix, we carried out a series of three separate variation partitionings (Borcard et al. 1992; see Fig. 1). The variation fractions represent the adjusted percentage of explained variation (R^2adj), which is not biased by the numbers of variables in the different sets of predictors (Peres-Neto et al. 2006). The significance of each of the unique components in explaining variation in community composition was tested by permutation of residuals (999 permutations) under the reduced model (Legendre and Legendre 1998). The bootstrap test of fractions, using the Matlab-library in Peres-Neto et al. (2006), was carried out in order to test whether the contributions of the unique fractions were significantly different from each other and thus whether one of the sets of variables explained significantly higher or lower amounts of the variation in community composition.

We used fourth-corner analysis (Legendre et al. 1997; Dray and Legendre 2008) to quantify and test the relationships between plant species dispersal/persistence traits and the LOCAL and LANDSCAPE characteristics of the sites in which the species occur. The fourth-corner analysis directly links a table Q (p × s) of s traits for p species to a table R (n × m), containing m characteristics of n sites, through a table L (n × p) containing the occurrence of p species at n sites. The fourth-corner statistic (Srlq) which is the matrix-product RLtQ (where Lt is the transposed table L) measures the link between each species trait in table Q and each site characteristic in table R. The significance of the link (Srlq) was tested according to model 1 in Legendre et al. (1997) by permuting (9,999 times) the presence–absence values within each column of table L in order to generate the null hypothesis (H0) that the occurrence of the species is unrelated to the LOCAL and/or LANDSCAPE characteristics. Rejecting H0 thus means that the occurrence of the species, in association with their traits, differs from random expectations. *P* values were adjusted for multiple testing using the Holm-correction. The traits were analyzed individually because the number of species for



which measurements were available differed between traits. Seed mass was excluded from the analysis because of its high correlation with epizoochorous dispersal potential (Pearson's $r = -0.926$, $P < 0.001$; see Table 1 in Supplementary material).

All statistical analyses, apart from the bootstrap test of fractions, were carried out in R (R Development Core Team 2010), using the packages spacemakeR, lmodel2, packfor, vegan and ade4.

Results

Community composition in relation to site and landscape characteristics

Forward selection retained all the descriptors within the LOCAL model [in decreasing order of importance: Age ($P < 0.001$), Tree_cov ($P < 0.001$), Grazing ($P < 0.001$), Area ($P = 0.001$) and Hab_div ($P = 0.007$); Table 1]. All the descriptors were also retained (all with $P < 0.001$) within the LANDSCAPE model (Table 1). The most important landscape descriptors of the composition of the present-day plant communities were the amounts of grassland in the historical landscapes (Grass_1835, Grass_1938). Only 13 of the 57 spatial descriptors (PCNMs) were retained in the spatial model (SPACE; Table 1). The PCNMs selected as the most important (PCNMs 1, 4, 6, 7, 9; all with $P < 0.001$; Table 1) represent predictors of spatial variation in community composition at the largest spatial scales.

Variation partitioning showed that the three predictor sets LOCAL, LANDSCAPE and SPACE explained 28.5% (R^2adj) of the total variation in community composition (Fig. 1a). The spatial fraction (SPACE) made the largest unique contribution to the total variation (10.8%), followed by the unique fractions of LOCAL (5.5%) and LANDSCAPE (3.9%). The highest shared fraction of the community variation was explained by SPACE and LANDSCAPE (5.1%).

When the variation in the grassland component (Grassland) was decomposed into the subsets (1) amount of grassland in the present-day landscape (Grassland-present), (2) amount of grassland in the historical landscape (Grassland-past) and 3) SPACE (Fig. 1c), 6.9% of the total community variation was explained by the amount of grassland in the historical landscape. The majority of this variation was structured at larger spatial scales. The unique effect of the amount of grassland in the historical landscape explained a significantly higher proportion of the community variation ($P \leq 0.01$; bootstrap test for fractions) than the unique effect of the present-day amount of grassland.

Dispersal and persistence traits in relation to site and landscape characteristics

Fourth-corner analysis revealed several significant associations between the dispersal and persistence traits of the grassland species and the LOCAL descriptors (Table 2). Grazing intensity was significantly positively correlated with wind dispersal potential and negatively correlated with plant longevity. Species with a high animal dispersal potential (Epizoo, Endozoo), as well the ability to build up a persistent long-term seed bank and produce large

Table 1 Forward selection of the variables explaining community composition

Variables	R^2adjCum[a]	F[b]	P[c]
LOCAL			
Age	0.025	3.818	<0.001
Tree_cov	0.049	3.903	<0.001
Grazing	0.068	3.191	<0.001
Area	0.079	2.339	0.001
Hab_div	0.086	1.815	0.007
LANDSCAPE			
Grass_1835	0.042	5.916	<0.001
Grass_1938	0.069	4.246	<0.001
Grass_2004	0.085	2.843	<0.001
Land_div_2004	0.097	2.456	<0.001
Land_div_1938	0.103	1.781	0.005
Land_div_1835	0.109	1.713	0.008
SPACE			
PCNM4	0.016	2.812	<0.001
PCNM1	0.028	2.403	<0.001
PCNM6	0.038	2.158	0.001
PCNM9	0.048	2.057	0.001
PCNM7	0.057	2.061	0.001
PCNM47	0.063	1.726	0.006
PCNM5	0.069	1.677	0.006
PCNM3	0.074	1.551	0.014
PCNM13	0.079	1.538	0.013
PCNM12	0.083	1.485	0.018
PCNM42	0.087	1.483	0.027
PCNM2	0.091	1.379	0.036
PCNM25	0.094	1.367	0.040

The reduced models are shown for each of the predictor sets LOCAL, LANDSCAPE and SPACE

See "Materials and methods" for variable abbreviations

[a] Cumulative R^2adj-values for the selected variables

[b] F statistic

[c] P value from permutation testing

numbers of seed, were over-represented in grassland patches with a low tree cover (Tree_cov). In contrast, clonally-spread, perennial plants were significantly associated with grasslands that are overgrown by trees. Grassland age (Age) was significantly positively correlated with wind dispersal potential and epizoochory and negatively correlated with plant longevity (Table 2), indicating that species with high long-distance dispersal potential were over-represented in the oldest grasslands while long-lived and clonal species are mainly found in the youngest grasslands (Fig. 3).

At the landscape scale, none of the six traits were significantly correlated with the percentage of grassland (within a 300-m buffer zone) in the present-day landscape (Grass_2004; Table 2; Fig. 2). In contrast, long-distance dispersal potential by wind and animals (Wind, Epizoo, Endozoo) showed significant positive correlations with the amount of grassland habitat in the landscapes that surrounded the sites of the present-day grasslands in 1835 (Grass_1835; Table 2; Fig. 2). Perennial species that are spread clonally and/or have a high seed production were mainly found in present-day grasslands that were surrounded by relatively small amounts of grassland in the historical landscape (Table 2; Fig. 2).

There were significant correlations between the dispersal traits and the landscape diversity in both the present and past landscapes (Table 2; Fig. 2). The directions of the correlations changed over time, shifting signs between the historical landscapes and the present-day landscape (Fig. 2). Epizoochory and wind dispersal potential were both significantly negatively correlated with the diversity of the landscape matrix in 1835 (Table 2; Fig. 2) while no significant correlations were detected between these long-distance dispersal traits and landscape diversity in 1938 or at the present day. Plant longevity showed a significant positive correlation with landscape diversity in 1835 that shifted to a negative correlation with present-day landscape diversity (Table 2; Fig. 2). Seed bank persistence was significantly positively correlated with Land_div_2004.

Discussion

Plant species distributions are determined by the availability of suitable habitats in space and time, and by the species' abilities to disperse and persist (Perry and Gonzalez-Andujar 1993; Ozinga et al. 2004; Wiegand et al. 2005). If species show a delayed response to rapid environmental change, the distribution of dispersal traits in present-day communities should reflect the past availability of dispersal sources and suitable habitats (Bullock et al. 2002; Herben et al. 2006). However, although a few earlier studies have shown that persistence traits are related to the spatial distribution of habitats in the past, similar linkages were not detected for long-distance dispersal traits (e.g., Hérault and Honnay 2005; Adriaens et al. 2006; Lindborg 2007).

The present study shows that the dispersal and persistence characteristics of plant species in grassland communities are explained by historical, rather than by current, landscape configurations and local management at the present day. The study used an integrated approach to quantify and test the direct linkages between species' dispersal and persistence traits, and the present and historical properties of the grassland sites and their surrounding landscape. We showed that the wind and animal dispersal potentials of plant species in present-day grassland

Table 2 Results of the fourth-corner analysis showing the correlations, positive (+) or negative (−), between the species' dispersal traits and characteristics of the grassland sites (LOCAL) and of the landscape surrounding the present-day grasslands (LANDSCAPE)

	Wind	Epizoo	Endozoo	Longev	SBank	SProd
LOCAL						
Grazing	+++			—		
Tree_cov		—	-	+++	—	—
Age	+++	+++		—		
Hab_div						
Area	+			-		
LANDSCAPE						
Grass_2004						
Grass_1938		++		—		
Grass_1835	+++	+++	+	—		—
Land_div_2004				—	++	+++
Land_div_1938				-		—
Land_div_1835	—	—		+++		++

See "Materials and methods" for variable abbreviations

Wind wind dispersal potential, *Epizoo* epizoochory, *Endozoo* endozoochory, *Longev* adult plant longevity, *SBank* seed bank persistence, *SProd* seed number per ramet

The number of the signs corresponds to the significance values (after Holm-correction): +++/— $P \leq 0.001$, ++/– $P \leq 0.01$, +/- $P \leq 0.05$, *blank* non-significant

communities were significantly positively associated with both grassland age and with the amount of grassland habitat in the historical landscape (Table 2; Figs. 2, 3). Long-distance dispersal processes no longer appear to be contributing to the colonization (dispersal and subsequent establishment) of grassland species in the available areas of habitat, with the structure of the modern landscape limiting effective dispersal between grassland sites (Schupp et al. 2010). The importance of seed dispersal for colonization appears to be declining in the increasingly isolated and overgrown grassland sites, and local communities are likely to become increasingly dominated by long-term persistent species.

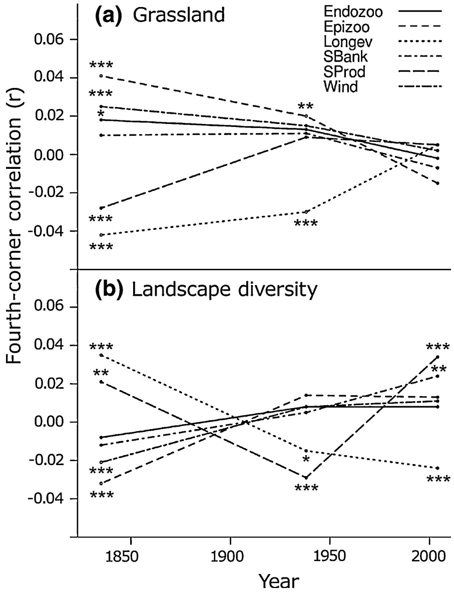


Fig. 2 Fourth-corner correlations between the six dispersal traits and **a** percentage of grassland and **b** diversity of the surrounding landscape at three time intervals: present-day (2004) and past (1835 and 1938). Significant relationships: ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$

Community composition: dispersal limitation at local and landscape scales

At the local scale, variation in community composition was mainly explained by factors related to long-term grazing continuity and tree cover (Age, Tree_cov; Table 1)—variables that have been shown to influence light availability (shading), litter accumulation and the long-term availability of suitable microsites for establishment (Eriksson 1995; Pacala and Rees 1998). Our finding that long-term grazing continuity explained higher amounts of variation than current grazing intensity (Grazing) and present-day grassland area (Area) suggests that levels of dispersal and subsequent establishment are likely to have been higher under historical management regimes.

At the landscape scale, community composition was mainly explained by the percentage of grassland habitat in the surrounding historical landscapes in 1835 and 1938 (Table 1; Fig. 1c). Because our study included grasslands

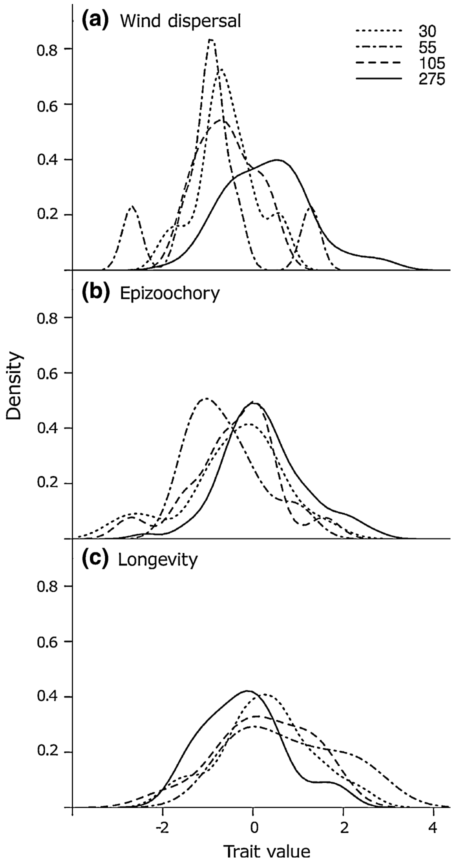


Fig. 3 Probability density plots showing the distribution of **a** wind dispersal potential, **b** epizoochory and **c** adult plant longevity for different grassland age classes (30, 50, 105 and 275 years of grazing continuity). Mean trait values (at the grassland polygon level) were standardized with mean = 0, SD = 1

that differed in their grazing continuity, we suggest that the amount of dispersal sources in the historical landscape not only influences the plant species composition of old (permanently grazed) grasslands but also that of young grasslands on previously arable sites. The significant association between species composition in old grassland sites and the distribution of dispersal sources in the historical landscape may reflect a time lag in species' response to habitat fragmentation (e.g., Helm et al. 2006). Plant species composition in grazed, previously arable (young) sites has also been shown to be dependent on the proximity to semi-natural grasslands in the historical landscape (Cousins and Aggemyr 2008; Reitalu et al. 2011), suggesting that grassland species have accumulated in the surrounding landscape over long periods of continuous grazing management.

In the present study, most of the variation in community composition that was explained by the landscape context within the 300-m buffer zone (LANDSCAPE) was spatially structured at larger scales (SPACE; >1.2 km; Fig. 1), suggesting that historical dispersal processes acting on spatial scales larger than 300 m—up to the extent of the whole study landscape, and probably even beyond—have influenced the present-day community composition. However, a large contribution to the total explained variation was made by the ("pure") spatial structure in community composition that is not related to the LANDSCAPE or LOCAL descriptors that we used in our study. This large, unique spatial component may be a reflection of dispersal-related factors (such as small habitats or dispersal sources in the landscape matrix) that were not characterized by the landscape descriptors. The unique spatial component may also, partly, reflect effects of unmeasured and spatially structured environmental factors (such as soil characteristics). However, the study of Reitalu et al. (2009), in the same study area, showed that gradients of edaphic variation are short and did not significantly explain variation in community composition.

The fact that the historical characteristics of the landscape and local management explained larger amounts of variation in community composition than the current landscape configurations and local management intensity at the present day, indicates that present-day grassland plant communities are dispersal limited at the landscape and the local scale (Bullock et al. 2002).

Long-distance dispersal processes are no longer effective in the present-day landscape

The results from the simultaneous (fourth-corner) analysis of data on dispersal traits, local and landscape characteristics (historical and present-day) and community composition show that plant species with a high long-distance dispersal potential by wind and grazing animals (Wind, Epizoo, Endozoo) are over-represented in present-day grasslands which have had a long history of continuous grazing management (Age) and in grasslands that were surrounded by a landscape containing large proportions of grassland habitat in the past (Grass_1835 + 1938; Table 2; Figs. 2 and 3). The grassland habitat in the historical surrounding landscape is expected to have acted as a dispersal source, while grazing continuity (Age), at the local scale, is expected to have ensured the long-term availability of gaps for establishment.

Animal dispersal potential was not associated with current grazing intensity (Grazing), but was instead negatively related to tree cover (Tree_cov), suggesting that the seed dispersal potential by animals, although reflecting dispersal and subsequent establishment under historical disturbance regimes (Age; Table 2; Figs. 2 and 3), may also be related to present-day light availability. Ozinga et al. (2004) suggested that sites with high light availability provide a higher food quality and thus contain more animal-dispersed species than more overgrown areas which contain many shade-tolerant species that are less attractive to herbivores.

In contrast to dispersal potential by animals, wind dispersal potential was associated (positively) with current grazing intensity and also with grassland area, suggesting that wind-dispersed species may still persist locally if there are enough gaps that can be colonized and if the grassland site is large enough.

The finding that long-distance dispersal traits are related to grassland age and to the amount of grassland habitat in the historical landscape, but not to the current landscape configuration, suggests that the colonization of grasslands by species that are dependent on long-distance dispersal is limited at both local and landscape scales at the present day (Poschlod and Bonn 1998; Verheyen and Hermy 2001; Bullock et al. 2002). However, wind- and animal-dispersed species can still persist at the local scale if the sites are open (less shaded), disturbed by grazing and/or sufficiently large.

Persistence traits: longer-lived species are found in isolated and abandoned sites

The negative correlation between adult plant longevity and the amount of surrounding grassland habitat in the historical—but not in the present-day—landscape indicates that long-lived species with the ability to spread clonally show a time lag in their response to habitat fragmentation and suggests that there is an extinction debt. These long-term persistent species are over-represented in present-day grassland sites that were already isolated in the historical landscape (cf. Lindborg 2007; see also Poschlod et al. 2011). Adult plant longevity was also negatively associated with grazing continuity (Age; Table 2; Figs. 2 and 3). Although grasslands on sites with a long continuity of grazing management contain many long-term persistent species, young grasslands on previously arable sites may contain an even higher proportion of long-lived, clonal species. However, the clonal species in younger grasslands include species (such as *Arrhenatherum elatius*, *Cerastium arvense*, *Festuca pratensis*, *Linaria vulgaris*, *Sanguisorba minor*) which have persisted from previous agricultural land use, or early stages of the succession to semi-natural grassland.

The fact that short-lived plants were more often found in intensively grazed than in abandoned, overgrown sites (Grazing and Tree_cov; Table 2) agrees with results from earlier studies that found relatively high proportions of short-lived species in grassland sites with high grazing pressure (e.g., Noy-Meir et al. 1989; McIntyre and Lavorel 2001). Species with short life cycles have been shown to have a high extinction risk over short time periods, because their population persistence depends on frequent recruitment (Pimm et al. 1988; Stöcklin and Fischer 1999). Our results, therefore, suggest that short-lived grassland species will respond rapidly (and negatively) to future habitat fragmentation and decreased grazing intensity.

Low seed production (SProd) was associated with large amounts of grassland area in the surrounding historical landscape in 1835 (Grass_1835; Table 2; Fig. 2). Seed production is a limiting factor for dispersal (Primack and Miao 1992). Our results suggest that species with low seed production are likely to have had higher levels of dispersal and establishment in the historical landscape than in the increasingly fragmented, present-day landscape, and that they have thus been more strongly affected by landscape fragmentation than species that produce many seeds (Tilman 1994). A highly heterogeneous landscape matrix at the present day (Land_div_2004) was associated with high seed production and short-lived species. A diverse present-day landscape matrix is likely to contain a range of habitats that can act as dispersal sources for generalist species (Jonsen and Fahrig 1997; Krauss et al. 2004), which mainly have short life cycles and/or produce large numbers of seed (Dupré and Ehrlén 2002). Seed bank persistence and seed production showed similar associations with the local (site) characteristics. The study by Saatkamp et al. (2009) demonstrated that the longevity index may not only reflect seed survival in the soil but is also likely to be influenced by seed input from the above-ground vegetation. The fact that seed bank persistence and seed production were significantly correlated in the present study (see Table 1 in Supplementary material) suggests that seed input from the current vegetation has made a substantial contribution to the values of the longevity index.

Conclusions

The use of an integrated approach which directly links quantitative traits to present-day and historical environmental descriptors, allows the identification of the key dispersal and persistence traits that determine species' responses to ongoing landscape fragmentation and changes in local management. Our results emphasise the role of landscape history as a determinant of the dispersal potential of plant species within present-day communities. The importance of long-distance dispersal processes has declined in the increasingly fragmented grassland habitats in the modern landscape, and it is likely that long-term persistent species will play a more dominant role in grassland communities in the future.

Our results also show that, even within a highly fragmented landscape, many species that have a high long-distance dispersal potential can still persist locally in the presence of grazing disturbance—which creates gaps that are available for establishment: these species are likely to become extinct in the future.

However, as long as long-distance-dispersed species are still present in the landscape, conservation measures that improve grassland connectivity, maintain a heterogeneous landscape matrix and ensure the availability of suitable microsites (gaps) may delay the repayment of the extinction debt (Kuussaari et al. 2009).

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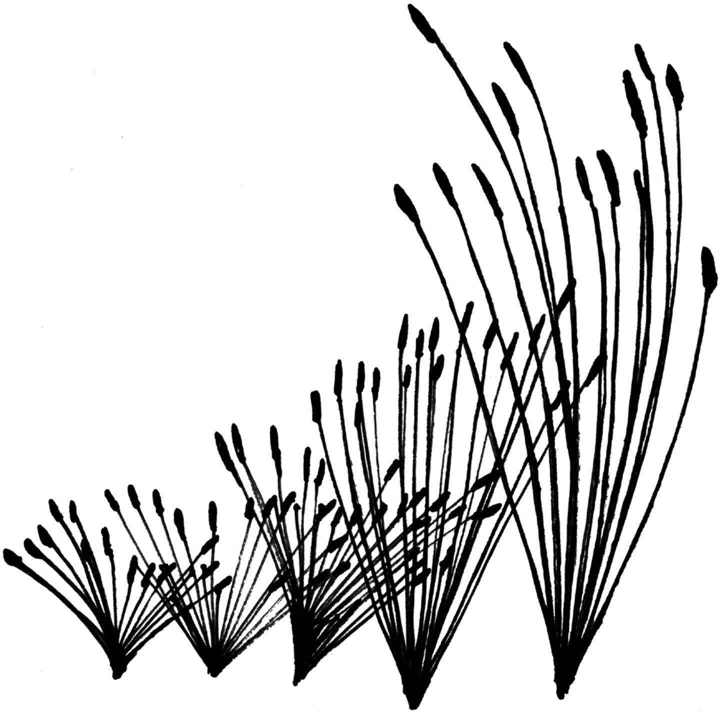
Supplementary material

Table 1 Pearson's product-moment correlations (r) between the seven dispersal and persistence traits. Wind: wind dispersal potential, Epizoo: epizoochory, Endozoo: endozoochory, Longev: adult plant longevity, SBank: seed bank persistence, SProd: seed number per ramet, SMass: seed mass. Significant relationships ($P \leq 0.05$) are indicated in bold text

	Epizoo	Endozoo	Longev	SBank	SProd	SMass
Wind	**0.502**	0.002	−0.082	**0.218**	**0.226**	**−0.545**
Epizoo		−0.02	**−0.18**	**0.513**	**0.276**	**−0.926**
Endozoo			0.039	0.266	−0.278	−0.139
Longev				**−0.477**	−0.13	**0.182**
SBank					**0.409**	**−0.52**
SProd						**−0.246**



III Drivers of dispersal trait diversity

Current and historical drivers of dispersal trait diversity in plant communities

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Abstract

The diversity of dispersal and persistence traits is a key aspect of biodiversity that will determine the response of plant communities to future habitat fragmentation and deterioration. Using quantitative information on long-distance seed dispersal potential by wind and animals and on species' persistence/longevity, we (1) tested whether observed patterns of multidimensional dispersal and persistence trait diversity (functional richness, FRic and functional divergence, FDiv) of semi-natural grassland plant communities differed from random expectations, given the species richness, and (2) quantified the extent to which current and historical landscape structure and local management history may act as filters that constrain trait diversity of plant communities within present-day grassland sites. Null model analysis revealed that more grassland sites than expected had trait diversity that was lower or higher than expected, indicating that the multivariate range and dispersion of trait values in present-day communities are influenced by deterministic filtering processes. Both FRic and FDiv increased with grassland age, suggesting that long-term grazing continuity has promoted the diversity of dispersal and persistence traits in present-day grasslands. We also found that FDiv was interactively affected by current grazing intensity and the amount of grassland habitat in the historical surrounding landscape in 1938: communities in sites that are well-grazed at the present-day, and were also surrounded by large amounts of grassland in the past had the highest diversity of dispersal and persistence strategies. The study suggests that the historical context of a site within a landscape will influence the extent to which current grazing management is able to maintain a diversity of dispersal and persistence strategies, and buffer communities (and their associated functions) against continuing habitat fragmentation.

Keywords: community assembly, functional divergence, functional diversity, functional richness, grassland plants, landscape fragmentation, life-history traits, persistence, phylogenetic autocorrelation, spatial autocorrelation

Introduction

Empirical and theoretical studies suggest that the current and ongoing loss of biodiversity is likely to have a negative effect on ecosystem functioning and stability in the face of future environmental change (Chapin et al. 2000; Loreau et al. 2001; Hooper et al. 2005; Isbell et al. 2011). It is the functional traits of the species, rather than the identities of the species themselves, that are expected to determine how ecological communities will respond to environmental change (Lavorel & Garnier 2002; Laliberté et al. 2010).

Land use change, habitat fragmentation and habitat deterioration are major threats to plant biodiversity at both global and local scales (Vitousek et al. 1997; Sala et al. 2000; Foley et al. 2005). The dispersal and persistence traits of their component species will determine the ways in which plant communities, and their associated functions, are able to track suitable habitat. Plant species are dispersed by multiple vectors in space (e.g. long-distance dispersal by wind and animals) and time (e.g. in the seed bank or as long-lived perennials) and show inter-specific differences in their dispersal potential for each of these vectors (Poschlod et al. 2005; Ozinga et al. 2009). If the species within a local community represent a wide variety of different dispersal and persistence strategies, the loss of a specific dispersal vector may be compensated for – if alternative dispersal mechanisms allow for successful colonization. The diversity of dispersal and persistence traits within plant communities therefore represents an important facet of biodiversity that is expected to determine how communities, and their associated functions, are sustained under future habitat fragmentation and changes in local management (see Mayfield et al. 2006).

Previous studies (Ozinga et al. 2004; Mayfield et al. 2006) of dispersal trait diversity have focussed on the number of dispersal syndromes and do not allow for interspecific variation of dispersal traits or the fact that dispersal potential is multidimensional. There is a need for studies that assess multivariate dispersal potential (especially in fragmented landscapes) and its response to environmental drivers (McGill et al. 2006; Villéger et al. 2008; Mouchet et al. 2010).

The range and dispersion of dispersal and persistence traits within local communities is constrained by a set of nested (hierarchical) filtering processes that act over a range of spatial scales (Keddy 1992; Zobel 1997). At the landscape scale, spatial isolation resulting, for example, from low amounts of suitable habitat in the surrounding landscape, acts as a filter that decreases rates of long-distance dispersal and colonization success (Eriksson et al. 2002), and may only allow a subset of species with a specific suite of dispersal traits to co-exist. At the local scale, a lack of suitable micro-sites may reduce the probability of successful colonization by seed and favour long-term persistent species (Grubb 1977; Bullock et al. 1995). Both local and landscape filters may act in concert (Bullock et al. 2002; Purschke et al. 2011) and generate communities that are characterized by a lower variety of different dispersal and persistence strategies than would be expected from a random draw of species from the regional species pool (trait convergence). However, if, for example, both landscape structure and the availability of gaps for establishment favour multiple alternative dispersal strategies, local communities will consist of species that have a wide variety of complementary dispersal and persistence strategies (cf. Grime 2006; Schleicher et al. 2011) and the observed diversity of dispersal and persistence traits will be higher than expected.

Dispersal filtering may also have an historical component. Dispersal limitation and long-term persistence have been shown to lead to a time lag in species' responses to habitat fragmentation and changes in local management regime (Helm et al. 2006; Herben et al. 2006). Previous studies have drawn attention to the importance of history as a determinant of dispersal potential in present-day plant communities, and have shown that the distribution of individual dispersal and persistence traits may be related to past rather than to present-day descriptors of sites and their surrounding landscape (Adriaens et al. 2006; Lindborg 2007; Purschke et al. 2011).

Analyses of the relationships between trait-derived indices, such as functional diversity, and environmental variables, are often limited by the presence of spatial and/or phylogenetic autocorrelation which may introduce bias in the estimation of model coefficients. It has recently been recognized that spatial structure and phylogenetic information should be considered jointly: trait-similarity between species may be the result of a shared evolutionary history; traits may also show recent convergence as a result of adaptation to similar environmental conditions in spatially adjacent sites (Diniz-Filho et al. 2007; Freckleton & Jetz 2009; Kühn et al. 2009).

The main aim of the present study was to assess the extent to which the diversity of dispersal and persistence traits in present-day semi-natural grassland plant communities is determined by the current and historical characteristics of local management regime and the configuration of the surrounding landscape. Semi-natural grasslands are among the most diverse habitats in Europe (Poschlod & WallisDeVries 2002; WallisDeVries et al. 2002), and long-distance dispersal by multiple vectors has been shown to be of central importance for the colonization and maintenance of species diversity in these grassland communities (Fischer et al. 1996; Tackenberg et al. 2003). However, the substantial reduction in the area of semi-natural grasslands over the last few centuries has led to a decline in the contribution of dispersal processes to colonization success in the present-day landscape (Poschlod & Bonn 1998; Schupp et al. 2010; Purschke et al. 2011).

The first objective of our study was to quantify the extent to which the dispersal and persistence trait diversity (multivariate functional richness and functional divergence) within the present-day grassland plant communities is higher or lower than expected from a random draw of species from the regional species pool – taking into account five quantitative dispersal and persistence traits. If there are dominant filtering processes that either restrict the distribution of traits or that select for alternative/complementary dispersal strategies, we expect that the observed functional diversity will, on average, be either less or greater than predicted. The second objective was to quantify the extent to which the configuration of the present-day and historical landscapes, the current management status, and the history of management may act as filters that constrain the dispersal trait diversity within the present-day communities – taking into account both spatial and phylogenetic autocorrelation. To what extent does the effect of local management status on dispersal trait diversity depend on the structure of the past and present landscape surrounding the grassland sites?

Material and Methods

Study area

The study area is situated on the Baltic Island of Öland and covers an area of approximately 22 km^2. The landscape has an overall flat topography and consists of a mosaic of grassland, arable fields and forests. The proportion of semi-natural grassland in the landscape has declined progressively over the last three centuries, from 86 % in 1723 to 9 % at present-day (Johansson et al. 2008).

Vegetation sampling

The presence-absence of herbaceous, vascular plant species was recorded between May and August 2007 in 113 grassland polygons (sites). Sampling was restricted to dry grassland vegetation with low levels of eutrophication, in order to avoid major gradients of edaphic variation (cf. Reitalu et al. 2009). In each grassland site we searched for all herbaceous vascular plant species within vegetation that contained the grasses *Festuca ovina* and/ or *Helictotrichon pratense*. Both of these species are wide-spread in mesic and dry grasslands and avoid eutrophicated habitats (Prentice et al. 2007). We did not sample the area within a 200-m zone along the polygon border in order to reduce edge effects (see Reitalu et al. 2008). Sampling time was proportional to the polygon area and ranged between 1-12 hours. A total of 185 species was recorded in the 113 polygons.

Local and landscape descriptors

Each grassland polygon was assigned to one of four age classes (Age), corresponding to 30, 55, 105 and 275 years of grassland continuity before 2004 (Johansson et al. 2008). Present-day grazing intensity (Grazing) was estimated on a scale of 0 to 4 (ungrazed to intensely grazed) on the basis of the presence of grazing animals and recent signs of grazing (see Reitalu et al. 2008). We also quantified the cover of trees (Tree.cov, in %) and the total area (Area, in ha) for each grassland polygon. The percentage of grassland habitat within the present-day and historical landscape (Grass.1835, Grass.1938, Grass.2004) within a 300-m buffer zone around the edge of each of the grassland polygons was quantified by Johansson et al. (2008), using historical maps from three different time periods, 1835, 1938 and 2004.

Dispersal and persistence traits

Quantitative information on five life-history traits related to long-distance seed dispersal and persistence was compiled from trait data bases (Poschlod et al. 2003; Kleyer et al. 2008). Long-distance dispersal potential was characterized by (1) wind dispersal potential (Wind), ranging from 0 (low) to 7 (high) on an ordinal scale, derived from data on seed terminal velocity and seed release height (Tackenberg 2003); (2) epizoochory potential (Epizoo), predicted from seed mass and seed morphology using the regression model proposed by Römermann et al. (2005); and 3) endozoochorous dispersal potential (Endozoo) on a continuous scale, estimated according to the approach of Bruun & Poschlod (2006). Persistence was characterized by (1) adult plant longevity (Longev), derived from data on plant life span and on clonal propagation, using three ordinal classes “annual and biennial”, “perennial/without the ability to spread clonally”, and “perennial showing clonality”; and (2) seed bank persistence (SBank), based on the longevity index (Thompson et al. 1997; Bekker et al. 1998).

Trait diversity indices

For each grassland site, multivariate trait diversity (including all five dispersal and persistence traits) was characterized by two indices, functional richness (FRic) and functional divergence (FDiv), according to the framework of Villéger et al. (2008). FRic is a measure of the multivariate range of trait values, or the functional space, occupied by species in the community. FDiv measures how species are distributed within this volume and thus to which degree species cluster at the edges of the trait space. Low FDiv values indicate that most species cluster around the center of the multivariate trait space, whereas high values indicate the predominance of species with extreme trait values that lie in the edges of the trait space. We did not estimate the third functional diversity component (functional evenness) of Villéger et al. (2008), because this measure of functional evenness performs poorly with presence-absence data (Mouchet et al. 2010). Because our study included both continuous and ordinal traits, and because trait data were not available for all species, FRic and FDiv were calculated according to the distance-based generalization of the original approach by Villéger et al. (2008), as implemented in the 'FD'-package (Laliberte & Legendre 2010) in R (R Development Core Team 2011). Calculations of FRic and FDiv were based on the set of 143 species (78 % of the total number of species) that were represented by data on at least three of the five traits.

Analysis

Null model analysis

We carried out null model analysis, to test whether the observed trait diversity values (FRic and FDiv) were simply a product of species richness, or whether there were underlying trait-based filtering mechanisms that caused that the observed values of functional diversity to be higher or lower than expected from a random draw of species from the species pool (Mason et al. 2007). Null communities were generated using the trial swap algorithm (Miklos & Podani 2004) in the R-package 'vegan' (Oksanen et al. 2011); swapping species occurrences among the grassland sites but keeping both the species richness at each site and the occurrence frequency of each species across the whole landscape constant. This null model approach takes into account the fact that a) the number of species in a grassland site will constrain the range of possible trait values and b) the species are dispersal-limited and the ability to colonize a grassland site will depend on a species' frequency in the study area. For each site, the trait diversity indices were recalculated for 999 randomizations to test whether the observed trait diversity values were significantly ($P < 0.05$) higher or lower than expected by chance. We calculated the standardized effect size (SES), defined as the ratio between observed to expected values of trait diversity: SES = (Obs - Exp)/sd(Exp), where Obs is the observed trait diversity value and Exp and sd(Exp) are the mean and the standard deviation of the expected trait diversity in the 999 random communities. The SES is independent of species richness (in our study: FRic: $r = 0.08$, n.s.; FDiv: $r = -0.12$, n.s.) and negative or positive SES values indicate that species in a local community are more similar or dissimilar, with regard to their dispersal and persistence trait values, than random expectations.

We tested whether the mean SES of the grassland sites differed from zero (one-sample *t*-test), in order to assess whether the trait diversity of the grassland sites was, on average, lower or higher than random expectations. The average functional diversity of the sites is assumed to be random if approximately 95% of the SES values fall within the range between -2 and 2 (Gotelli & Rohde 2002). We also tested whether the number of grassland sites that had significantly higher or lower trait diversity values than expected (from the 999 random communities) was greater than expected, using a one-tailed binomial test. SES values, instead of the observed FRic and FDiv values, were used in all the subsequent analyses.

We used principal component analysis (PCA) to visualize whether high or low values for FRic and FDiv were related to specific trait values. PCA was carried out on the community-level mean trait values, and FRic- and FDiv-vectors were projected onto the trait values using the *envfit*-function in 'vegan' (Oksanen et al. 2011). This ordination of site-level trait mean values and functional diversity does not allow the visualization of within-site variation in trait values.

Drivers of diversity in dispersal and persistence traits

We used GLM regression analyses to quantify and test the relationships between dispersal/persistence diversity (SES of FRic and FDiv) and the historical and current descriptors of the grassland sites and their surrounding landscape. All explanatory variables were scaled to mean = 0 and SD = 1 prior to analysis. Absolute Pearson correlation coefficients, $|r|$, between explanatory variables did not exceed 0.3 (see Table S1 in the Appendix). In order to test for possible non-linear effects (Reitalu et al. 2010; Pakeman 2011), as well as the possibility that the effect of local management on trait diversity may depend on landscape context (Rundlöf & Smith 2006), we ran a series of separate models to select significant quadratic effects, and significant two-way interactions between the local and landscape descriptors. To obtain the minimal adequate model that best described the data, we then carried out a stepwise backward variable selection procedure on the full model, including all linear effects as well as the pre-selected significant quadratic effects and two-way interactions from the a-priori selection. Quadratic effects in the final, reduced model were only reported if the lowest or highest value of the quadratic curve was within the range of values of that explanatory variable (tested using the Mitchell-Olds & Shaw (1987)-test in 'vegan' (Oksanen et al. 2011)).

We checked, and if necessary, corrected for spatio-phylogenetic autocorrelation in the residuals of the minimal adequate model using the spatio-phylogenetic eigenvector filtering approach proposed by Kühn et al. (2009). First, the phylogenetic distance between the sites (phylogenetic beta diversity) was assessed by the phylosor index (Bryant et al. 2008), R-package 'picante' (Kembel et al. 2010)) which is defined by the fraction of branch-length shared between two communities. We used a phylogeny based on a published (topological) supertree for Central European angiosperms without branch length information (Durka, 2002; with updated topology). We dated the internal nodes of the tree with the help of an extensive literature survey on published ages of the respective branching events. An ultrametric tree was created by distributing the nodes that lacked dating information evenly between the dated nodes using the 'bladj' algorithm in Phylocom (Webb et al. 2008). Second, the phylogenetic similarity matrix was converted into a dissimilarity matrix which was decomposed into its eigenvectors using principal coordinate analysis (PCoA) in the R-package 'ape' (Paradis et al. 2004). The set of 47 eigenvectors that corresponded to positive eigenvalues were used as predictors for phylogenetic information structured at different spatial scales. Finally, we selected spatio-phylogenetic eigenvectors that reduced residual autocorrelation in the minimal adequate non-spatial models below a significance level of alpha=0.05, using Moran eigenvector filtering (Dray et al. 2006) and the ME-function (modified by I. Kühn) in the R-package 'spdep' (Bivand et al. 2011). The selected eigenvectors were included as co-variables in the minimal adequate regression models in order to correct for spatio-phylogenetic autocorrelation.

Results

Null model analysis

Null model analysis revealed that the mean standardized effect size of functional richness (FRic) was not significantly different from zero (Fig. 1, Table 1), indicating that the multivariate range of dispersal and persistence traits within the grassland sites is, on average, not significantly higher or lower than expected from random. However, the values of functional richness were highly variable across the landscape, and there were more grassland sites than expected that contained communities with significantly lower (n=9) or higher (n=10) than the expected functional richness (Table 1). In contrast to FRic, the mean standardized effect size of functional divergence (FDiv) was on average higher than expected (Fig. 1, Table 1), indicating a general tendency for species within the grassland sites to have higher levels of distinct/alternative dispersal and persistence strategies than expected from a random draw of species from the regional species pool. A higher than expected number of sites (n=10) contained communities with a greater than expected functional divergence, but only few sites (n=4) contained communities that had significantly lower than expected FDiv values.

Relationships between dispersal trait diversity and local, landscape and historical filters

The minimal adequate models for both FRic and FDiv had spatially non-independent residuals (Table 2). This residual autocorrelation was removed by the inclusion of pre-selected spatio-phylogenetic filters in the regression models.

None of the dispersal trait diversity indices (SES of FRic and FDiv) was significantly explained by current landscape configurations (Grass_2004) or grassland area (Area). Instead, both FRic and FDiv were significantly positively associated with grassland age (Age, Table 2), indicating that the multivariate range of dispersal and persistence traits that is occupied by the species, as well as the degree to which species within local communities have alternative/distinct dispersal and persistence strategies, are higher in older grassland sites that have been continuously grazed over long periods of time. FRic was also strongly negatively associated with the percentage cover of trees within the sites (Tree_cov). In addition, FDiv showed a significant positive association with the percentage of grassland habitat in the surrounding

Table 1. Mean standardized effect sizes (SES) for functional richness (FRic) and functional divergence (FDiv, significance levels from one-sample *t*-tests) and the number of communities (n=113 in total) that had FRic and FDiv values lower or higher than expected from 999 random communities (significance levels from one-tailed binomial test). *** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05; n.s., non-significant.

	FRic	FDiv
Mean SES	0.047 n.s.	0.394 **
Lower than expected (n)	9 **	4 n.s.
Higher than expected (n)	10 ***	10 ***

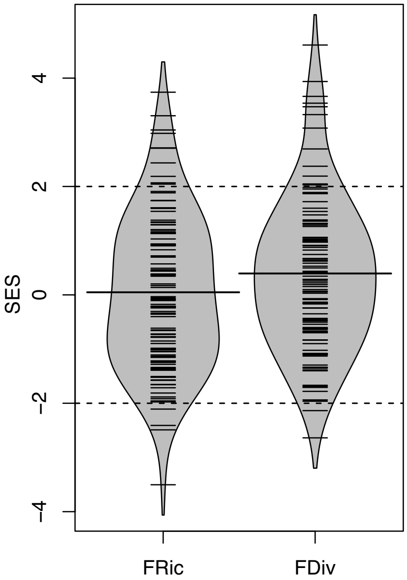

Fig. 1. Bean plots (combining density and strip plots) showing the distribution of standardized effect size values (SES) for functional richness (FRic) and functional divergence (FDiv). Strips depict the individual observations (n=113 communities) and thick lines indicate the mean. Density kernels were estimated based on the individual SES values. Negative or positive SES-values indicate that the trait diversity is lower or higher than expected. Strips outside the range (-2; 2) indicate communities that have trait diversity values that are significantly different from those estimated from 999 random communities.

Table 2. Minimal adequate regression models (GLMs) of the relationship between the standardized effect size of the dispersal trait diversity indices (FRic and FDiv) and the current and historical descriptors of the grassland communities and their surrounding landscape. The non-spatial models (Non-spatial) and the models including spatially-structured phylogenetic filters (Spatio-phylo) are presented. AIC, Akaike information criterion; *R^2adj*, adjusted R^2. *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; n.s., non-significant.

	FRic		FDiv	
	Non-spatial	Spatio-phylo	Non-spatial	Spatio-phylo
Intercept	-0.168 n.s.	-0.109 n.s.	0.332 **	0.332 **
Grass.1938			0.475 ***	0.413 **
Grass.2004			-0.402 **	-0.248 n.s.
Age	0.234 n.s.	0.271 *	0.293 **	0.356 **
Grazing			-0.353 **	-0.188 n.s.
Tree.cov	-0.656 ***	-0.545 ***		
Tree.cov^2	0.218 *	0.158 n.s.		
Grazing × Grass.1938			0.457 ***	0.463 ***
Global Moran's I	0.023 *	0.001 n.s.	0.024 *	0.006 n.s.
Filters		P1		P3
AIC	381.35	356.05	374.7	364.6
R^2adj	0.187	0.355	0.239	0.31

landscape in 1938 (Table 2). However, FDiv was mainly explained by the interaction between the percentage of grassland in the surrounding historical landscape in 1938 and the current within-site grazing intensity (Grazing × Grass.1938; Table 2, Fig. 2). FDiv increased with grazing intensity, but only if the sites were surrounded by a large proportion of grassland habitat in the historical landscape, indicating that grassland communities in currently well-grazed sites that were also well connected in the past contain species that have high levels of distinct/alternative dispersal and persistence strategies.

Discussion

Communities and their associated functions may be more resilient to environmental change if the species comprising the communities have the potential to disperse and persist by a wide range of different mechanisms (Mayfield et al. 2006; Ozinga et al. 2009). But what factors determine the diversity of dispersal and persistence traits in local communities?

The present study quantified the extent to which multivariate dispersal and persistence trait diversity in plant communities is explained by the current and historical characteristics of grassland sites and their surrounding landscape. Trait diversity was highest in sites that had a long grazing

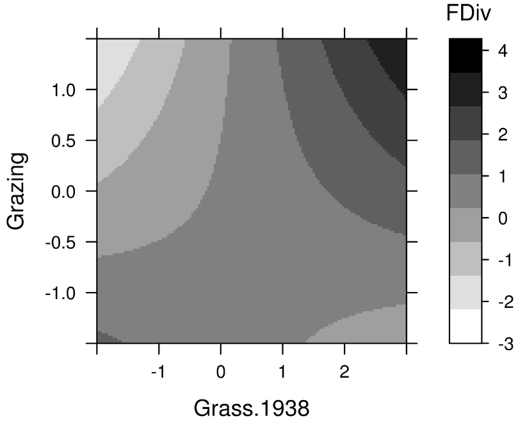

Fig. 2. Dispersal trait diversity (SES of FDiv; light grey to black shading) in response to the interaction between present-day grazing intensity (Grazing) and amount of grassland in the historical landscape (Grass.1938).

continuity, and in sites that were surrounded by large amounts of grassland habitat in the historical landscape in 1938. Dispersal trait diversity also showed a positive response to current grazing intensity – but only in sites that were well connected in the historical landscape. Successful dispersal by multiple vectors within the historical landscape, as well as the long-term availability of suitable microsites (gaps) for establishment within sites, are likely to have contributed to a high diversity of dispersal and persistence strategies within the present-day grassland sites.

Null model analysis

In order to assess whether there are filtering processes that either constrain the diversity of dispersal or persistence traits or select for alternative dispersal and persistence strategies, the observed trait diversity values need to be compared with the trait diversity values generated by a null model (Gotelli & Graves 1996). Because the null model used in our study maintained both levels of species richness within sites as well as species frequencies across the whole study landscape, the detection of higher or lower than expected trait diversity values provides a conservative indication of the presence of filtering processes (Gotelli & Entsminger 2003; Kembel & Hubbell 2006).

The observed values of functional richness (FRic) were on average not significantly different from random expectations, with a mean standardized effect size close to zero (Table 1, Fig. 1), indicating that there are no dominant filtering processes that either consistently constrain the multivariate range of dispersal and persistence traits or consistently select for species that differ in their dispersal and persistence strategies. However, the fact that communities in a significant number of sites were assembled non-randomly with respect to their dispersal and persistence traits suggests that there are trait-based filtering processes whose relative importance varies with varying environmental conditions (e.g. management intensity or landscape complexity) within the study system (Kembel & Hubbell 2006; Pakeman et al. 2011). More grassland sites than expected had significantly higher or lower FRic values than predicted from random communities (Table 1). Whereas the local habitat and landscape characteristics of some sites are likely to have acted as filters that restrict the multivariate range of dispersal and persistence traits, a different set of habitat characteristics in other sites may select for species with a wider range of (distinct) dispersal and persistence strategies. Lower than expected levels of trait diversity in some sites, combined with higher than expected trait diversity in other sites, appear to have resulted in average levels of trait diversity across the landscape that do not deviate from random predictions (Schamp & Aarssen 2009).

In contrast to FRic, FDiv was on average higher than expected (Table 1). The fact that more sites than expected (n=10) had significantly greater than expected FDiv, whereas only four sites had a lower than expected FDiv suggests that, across the grassland sites within our study system, there is a predominance of filtering processes that select for species with distinct/alternative dispersal and persistence strategies.

Drivers of dispersal trait diversity

The best model explaining the functional divergence of dispersal and persistence traits (SES of FDiv) included descriptors of current and historical management regimes, and landscape history. FDiv measures the extent to which between-species differences in dispersal and persistence traits are a reflection of extreme trait values. In our study, FDiv increased with both, grassland age (Age) and the percentage of grassland habitat in the historical surrounding landscape in 1938 (Grass.1938; Table 2). Long grazing continuity is likely to have ensured the long-term availability of gaps for establishment once seeds have arrived at a site, and may also allow for regeneration from the soil seed bank (Grubb 1977; Kahmen & Poschlod 2008). And the reserves of grassland habitat in the surrounding landscape represent the main dispersal source for the colonization of grassland fragments (Snäll et al. 2004). An earlier study in the same area (Purschke et al. 2011) showed that long-dispersal potential by wind and animals was explained by historical rather than by current landscape characteristics, and concluded that long distance dispersal processes no longer contributed to the colonization of the remaining grassland fragments within the increasingly fragmented modern landscape. In the present study, communities with high FDiv-values were associated with high mean values for long-distance dispersal potential by wind and animals, and lower adult plant longevity (Fig. 3). The fact that FDiv tended to be greater than expected in the oldest sites (the sites with the longest grazing continuity), as well as in sites that were surrounded by large amounts of grassland habitat in the past, suggests that (a) the historical landscape structure has promoted dispersal by multiple vectors, and (b) the presence of suitable microsites over long periods of time has ensured that these species could establish – generating communities that contain species that have a wide range of different dispersal and persistence strategies.

Although there was no direct association between FDiv and current grazing intensity, there was a highly significant interaction effect of present-day grazing intensity and the amount of grassland habitat in 1938 (Grazing × Grass.1938; Table 2, Fig. 2) on FDiv. Despite reduced levels of external recruitment in the modern landscape, grazing may allow the persistence of populations of long-distance dispersed species in the grassland fragments - possibly because small scale disturbance provides safe sites for continued internal recruitment (Purschke et al. 2011). But the results from the present study suggest that present-day grazing management will only be able maintain a high diversity of dispersal and persistence strategies in sites that were surrounded by large amounts of grassland habitat in the historical landscape.

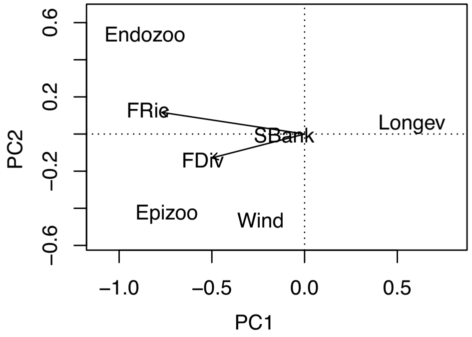

Fig. 3. Biplot from a principal component analysis (PCA) visualizing the relationship between the site-level (n=113) mean values of the five dispersal and persistence traits and the dispersal trait diversity indices (SES of FRic and FDiv) in the sites. The directions of the arrows indicate positive correlations between trait diversity and the respective trait.

FRic, a measure of the multivariate range of dispersal and persistence traits, was explained by grazing continuity and tree cover. FRic values were lower than expected in the youngest grassland sites, and in sites that are overgrown by trees. Low levels of FRic in the youngest grasslands are associated with a low proportion of long-distance dispersed grassland species (Fig. 3). In contrast, accumulation of litter and relatively high levels of shading within sites with high tree cover are likely to have selected for long-term persistent species (Fig. 3).

Conclusions

The results of the present study emphasize the importance of both history and current management regime (and their interactions) as determinants of multivariate dispersal and persistence trait diversity. Grazing continuity over long time periods enhances the diversity of different dispersal and persistence strategies within grassland communities. Trait diversity increases with current grazing intensity, but only in sites that were well-connected to grassland areas in the past. The extent to which local grassland management strategies will be able to maintain a diversity of dispersal traits and buffer communities, and their associated functions, against future environmental changes is likely to depend on the historical context of sites within the landscape.

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Supplementary material

Table S1. Pearson's product-moment correlations (*r*) between seven explanatory variables. Significant correlations are indicated by bold text.

	Grass.1938	Grass.1838	Area	Tree.cov	Grazing	Age
Grass.2004	0.25	-0.10	0.16	0.04	0.16	-0.06
Grass.1938		0.19	0.02	-0.05	0.14	0.25
Grass.1838			0.03	-0.09	0.23	**0.3**
Area				0.05	0.21	0.18
Tree.cov					-0.25	0.16
Grazing						0.18

IV Plant functional trait responses

Plant functional responses to local, landscape and historical factors in semi-natural grasslands

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Abstract

Abandonment of traditional management has led to a severe decline of semi-natural grasslands and their biodiversity throughout Europe. To understand and predict the effects of land-use change on plant biodiversity in these ecosystems, taxonomic indicators should be complemented by functional trait based indicators. We assessed the functional composition (community weighted mean, CWM and functional divergence, FD) in 475 50 × 50 cm semi-natural grassland plots, and quantified the extent to which CWM and FD are explained by past and present levels of local grazing management and the present and historical characteristics of the surrounding landscape, taking spatial autocorrelation into account. The CWM and FD within the grasslands were strongly associated with current grazing intensity, but also with local management history and the historical structure of the surrounding landscape. The association between community functional composition and the historical structure of the landscape indicates a time-lag in plant trait responses to the loss of grassland habitat. The functional composition in grassland patches in the fragmented present-day landscape still reflects their context within a vanished landscape – where the presence of extensive grasslands in the surroundings provided a diverse pool of grazing tolerant species. The results of the study suggest that information on landscape history and on the local species pool is likely to contribute to improved predictions about grassland functional responses to environmental change.

Keywords: biodiversity loss, community weighted mean, functional divergence, grazing, history, land use, semi-natural grasslands

Introduction

Semi-natural grasslands are among the most species-diverse ecosystems in Europe (Eriksson *et al.* 2002; Poschlod & WallisDeVries 2002; WallisDeVries *et al.* 2002). Traditional farming methods, including hay making and extensive grazing, have been essential factors in shaping the high diversity in semi-natural grasslands. Abandoned semi-natural grasslands normally exhibit lower plant species diversity (Kull & Zobel 1991) as a result of the encroachment of a relatively small number of more competitive species (Haeggström 1990; Pärtel *et al.* 1999). The ongoing abandonment of traditional management practices, which started in the last century, and the increasing fragmentation of the remaining grassland habitat represent a major and continuing threat to grassland biodiversity (Pakeman 2004; Pärtel *et al.* 2005; Billeter *et al.* 2008; Reitalu *et al.* 2009; de Bello *et al.* 2010).

The majority of studies of the impact of landscape structure, management and environmental variables on plant communities in semi-natural grasslands have concentrated on diversity indices, such as species richness (e.g. Bruun 2000; Lindborg & Eriksson 2004; Johansson *et al.* 2008) or evenness (e.g. Fischer & Wipf 2002; de Bello *et al.* 2006; Reitalu *et al.* 2009) that are based on species taxonomy. However, the concept of species diversity not only embraces the numbers of taxonomically defined species but can also be seen as including the functional properties of communities of species (e.g. Noss 1990; Magurran 2004; Harrington *et al.* 2010). Functional traits are characteristics of organisms that have demonstrable links to the organisms' function (Lavorel *et al.* 1997; Harrington *et al.* 2010), and an increasing number of studies, especially on plants, have focussed on the dynamics of functional traits, as a complement to changes in the taxonomic composition of communities (Lavorel *et al.* 1997; Westoby 1998; Lavorel & Garnier 2002; Cornelissen *et al.* 2003). Plant species diversity at a specific site is assumed to be a consequence of selective processes acting on traits (Lavorel & Garnier 2002; Shipley 2010). This selection will often, at least in temperate plant communities, favour a relatively small group of dominant species, with a combination of traits that are a reflection of the selective forces acting within a particular environment (Grime 1998; Martin *et al.* 2009). The assemblage of dominant species, with their trait expressions, can therefore be expected to provide a description of the response of semi-natural grassland communities to changes in local environmental conditions, landscape structure and management practices (Garnier *et al.* 2004; Martin *et al.* 2009).

The functional composition of plant communities can be described using two complementary metrics: (i) the community weighted mean (CWM), which is determined by the most abundant traits in a community and (ii) functional divergence (FD), which characterizes the dissimilarity of trait values within the community (de Bello *et al.* 2006; Lavorel *et al.* 2008; Vandewalle *et al.* 2010). CWM and FD are increasingly used to describe the functional composition of biotic communities and its responses to specific factors (Díaz *et al.* 2007a; Mason *et al.* 2007; Petchey & Gaston 2007; Lavorel *et al.* 2008; Moretti *et al.* 2009). However, few studies have attempted to untangle the responses of CWM and FD to multiple environmental factors (but see Mokany *et al.* 2008; Lavorel *et al.* 2011), and the consideration of historical factors is even rarer (but see Quétier *et al.* 2007).

In the present study, we assessed the ways in which the functional composition (CWM and FD) of semi-natural grassland plant communities responds to current and historical characteristics of the grassland sites and their surrounding landscape.

Current grazing and habitat structure have been previously identified as important drivers of trait composition and diversity within plant communities (McIntyre & Lavorel 2007; de Bello *et al.* 2010). However, despite increasing recognition of the impact of historical management and landscape structure on present-day diversity (Lindborg & Eriksson 2004; Helm *et al.* 2006; Gustavsson *et al.* 2007; Pärtel *et al.* 2007; Reitalu *et al.* 2009), historical factors are seldom included in studies of the functional composition of communities (but see Lindborg & Eriksson 2005; Lindborg 2007; Quétier *et al.* 2007). This gap in knowledge might be explained by the lack of historical data or the difficulties inherent in finding good proxies for characterizing historical management. However, if community composition shows a time lag in response to environmental changes – as is implicit in the concepts of “relaxation time” (Diamond 1972), “extinction debt” (Tilman *et al.* 1994) and “evolutionary history of grazing” (Milchunas *et al.* 1988) – historical effects should also be expected to influence the functional composition of plant communities. Historical filters should act by increasing or decreasing the size and functional composition of the pool of species available in a given region (Diaz *et al.* 2007b).

The main aim of the study was to quantify the extent to which current and historical landscape configurations as well as present-day and historical management status of the grassland sites may explain the CWM and FD of key plant functional traits, which are potentially linked to plant species’ response to environmental changes (Cornelissen *et al.* 2003) and/or may affect ecosystem processes (de Bello *et al.* 2010, Pakeman *et al.* 2011). Is there a time lag of plant functional response to historical changes in local management regime and landscape structure?

Material and Methods

Study area

The study area is situated in the central part of the Baltic island of Öland in south-eastern Sweden (centred on 56º40’N, 16º33’E) and covers an area of ca. 22 km^2. The climate is temperate with a mean annual temperature of 7ºC, a July mean of 17ºC and a January mean of -1ºC (Alexandersson *et al.* 1991). Mean annual precipitation is low (400 mm). The bedrock consists of Cambro-Silurian limestone and the overall topography is flat.

A previous study based on land use maps and aerial photographs for the time periods 1800, 1835, 1938 and 2004 (Johansson *et al.* 2008) provides a historical characterization of each of the remaining semi-natural grassland fragments in the present-day landscape. At the present day, semi-natural grassland fragments cover only 9 % of the landscape in the study area, compared with 86 % at the beginning of the 18th century (Johansson *et al.* 2008). Grassland fragments representing different age classes are scattered throughout the study area, and are interspersed with areas of arable cultivation and deciduous forest (Prentice *et al.* 2007; Johansson *et al.* 2008).

Vegetation data

An earlier study of the vegetation within the Jordtorp area (Prentice *et al.* 2007) showed that the two main gradients of variation in overall grassland community composition could be interpreted in terms of soil moisture and eutrophication. In the present study, vegetation sampling was based on a standardized sampling strategy that avoided major edaphic variation – only areas of dry grassland vegetation with low levels of eutrophication were sampled (cf. Reitalu *et al.* 2008). Vegetation data were collected in 475 (50 × 50 cm) plots in 121 grassland patches (1-10 plots per patch). Within each plot, species abundance was estimated as the sum of species occurrences in 25 (10 × 10 cm) subplots. A total of 217 species (belonging to 42 vascular plant families) was recorded. Soil analyses carried out on a random subset of 66 plots out of the 475 plots confirmed that soil moisture and nutrient content had no significant effects on species diversity (Reitalu *et al.* 2009).

Management intensity and habitat context

All the 475 plots were previously characterized, by Johansson *et al.* (2008) and Reitalu *et al.* (2008), by a range of different environmental and landscape descriptors. Grazing intensity was scored in the field by Reitalu *et al.* (2008), on a scale from 0 (no signs of present-day grazing by domestic animals) to 4 (well-grazed at the present-day). The levels of encroachment by shrubs and trees were estimated in the field as the percentage cover of shrubs and trees within each grassland patch by Reitalu *et al.* (2008). The management continuity of the grassland patches containing the vegetation plots was assigned, using GIS overlay-analyses (Johansson *et al.* 2008), to one of the four age categories (defined as years of continuous grazing management before 2004): 280, 105, 55 and 30 years. Past and present percentage cover of grassland and past and present percentage cover of forest were measured within a 200 m buffer zone around each plot (Johansson *et al.* 2008). The percentage of surrounding grassland was assessed for four time periods (2004, 1938, 1835 and 1800) and the percentage of forest for three time periods (2004, 1938 and 1835).

Plant trait data

Traits were measured in the field and in the lab for the 61 most abundant species (belonging to 21 families, see Appendix 1) in the study area. The list of these 61 dominants included more than 75% of the total number of species that occurred in the 475 plots. These dominant species were assumed to be functionally important because, together, they account for the majority of the biomass (see Quested *et al.* 2007 and Lavorel *et al.* 2008). Trait data were measured in 16 grassland patches well scattered through the studied landscape. Ten functional traits were measured for all 61 species following standardised protocols (Cornelissen et al. 2003): canopy height (both natural and stretched), reproductive height (both natural and stretched), lateral spread, leaf size, specific leaf area (SLA), leaf dry matter content (LDMC), leaf toughness and seed mass (see Table 1). Within each of the 16 grassland patches, five quadrats were established to select the individuals (1 per quadrat) to be measured. The first quadrat within the patch corresponded to the vegetation sampling plot laid out by Reitalu et al. (2008) that was included in the present data set. The remaining four quadrats were positioned randomly within the patch, but with the requirements that they should be separated from each other, and from the first quadrat, by a minimum distance of 2 m, and that they should be a minimum of 3 m from the patch border. The centre of each quadrat was marked. For each of the 61 species that occurred in the quadrat, we selected the individual that was closest to, but not further than 40 cm from, the central point. Traits were measured only on fully developed plants that showed no evidence of herbivory or parasitism and, where possible on flowering individuals. Fieldwork was carried out in 2006 and, because the 61 plant species represented a range of phenologies (i.e. spring and summer flowering), the fieldwork was divided into two campaigns (15th May to 21st June and 24th June to 2nd August). In total we measured traits on 1644 individuals.

Measures of functional composition

The functional composition of communities was assessed using two metrics: CWM and FD (Mason *et al.* 2003; Lepš *et al.* 2006). CWM was calculated for each species trait as the average of the trait values in the community, weighted by the relative abundance of the species carrying each value (Garnier *et al.* 2004; Violle *et al.* 2007):

$$1)\quad CWM = \sum_{i=1}^{S} p_i x_i$$

where x_i is the trait value of the i-th species (the average over all trait measures (maximum 80) for a given species) and p_i is the proportion (relative abundance) of that species. The CWM reflects the trait values of the dominant species in a community. The FD was calculated for each trait using the Rao index of diversity (Rao 1982; Botta-Dukat 2005; Ricotta 2005; Lepš *et al.* 2006; Lavorel *et al.* 2008) defined as:

$$2)\quad FD = \sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij} p_i p_j$$

where d_{ij} expresses the dissimilarity between species i and j according to their trait values, and p_i and p_j are the proportions (relative abundances) of the i-th and j-th species. The FD index represents the sum of the dissimilarities in trait space between all pairs of species, weighted by the product of the species' relative abundances. The Excel® Macro by Lepš *et al.* (2006; http://botanika.bf.jcu.cz/suspa/FunctDiv.php) was used to calculate the two indices.

Statistical analyses

Multivariate regression was used to test and quantify the effects of the eleven explanatory variables on the measures of functional composition (FD and CWM) for each of the ten traits. The interdependence between all pairs of explanatory variables was checked prior to analysis (see Appendix 2).

Species data and trait measurements collected from adjacent sites often have similar values and this may lead to spatial autocorrelation (SAC) in the model residuals (Hurlbert 1984; Legendre 1993; Beale *et al.* 2010). In standard regression analysis, the presence of SAC may lead to inflated Type I error rates (Legendre 1993) and can even invert the sign of the regression coefficients (Kühn 2007). Spatial autocorrelation was handled in the regression analyses according to the procedure proposed in Dormann *et al.* (2007): (1) for each of the twenty response variables we ran a full non-spatial linear model including all eleven explanatory variables; (2) the degree of SAC in the residuals of each of the full linear models was assessed by the Moran's I statistic; (3) the maximum spatial distance at which SAC was significant was quantified with the help of correlograms; (4) spatial weights matrices, based on the distance quantified in step 3, were generated; (5) the spatial weights matrices incorporating the spatial autocorrelation structure were included in simultaneous autoregressive models ($\mathrm{SAR}_{\mathrm{error}}$). Finally, we ran manual backward model selection using likelihood ratio tests in order to obtain the minimal adequate model for the FD and CWM for each trait. A global Moran's I test was carried out on each minimal adequate model to check whether SAC had been removed from the model residuals.

All statistical analyses were carried out using the packages "spdep" and "pgirmess" in the R Statistical Package, version 2.13.2 (R Development Core Team 2011).

Results

Present-day grazing intensity was the factor that showed the strongest association with the functional composition of the grasslands – influencing the largest number of traits in terms of both mean trait values (CWM) and functional divergence (FD) (Table 2). Dominant species in well-grazed grasslands were shorter (CWM of canopy and reproductive heights) and their leaves were characterized by a lower mean LDMC and lower mean toughness than dominant species in grasslands with lower grazing intensity. Higher grazing intensity was associated with higher FD in lateral spread, natural reproductive height, leaf area and seed mass within the communities. In contrast, well-grazed sites showed lower FD in terms of stretched canopy height and stretched reproductive height (Table 2).

In addition to the known effects of landscape context on vegetation composition at our site (Reitalu *et al.* 2009), the functional composition of the vegetation was also affected by the vegetation surrounding the sampled plots within the grassland patches (Table 2). Shrub cover around the plots was significantly positively associated with the FD of natural canopy height and with the FD of seed mass. In addition, while the mean values of lateral spread and leaf size were higher in the vegetation plots that were surrounded by high shrub cover, the mean trait values of SLA and toughness were higher in open grassland patches. The cover of trees was significantly negatively associated with the FD of toughness and positively associated with the mean of LDMC (Table 2).

Functional composition was also related to the context of the grassland patches within the landscape, with the majority of the significant associations between FD or CWM being with the surrounding land-cover in the historical, rather than the present-day, landscape (Table 2). The percentage of surrounding grassland area in 1800 was significantly associated with a large number of measures of functional composition: significantly negatively associated with the mean values of natural and stretched canopy height, natural and stretched reproductive height, leaf size and LDMC; and significantly positively associated with the FD of toughness (Table 2). Finally, the FD of both leaf size and specific leaf area (SLA) was significantly positively associated with grassland age (Table 2).

Discussion

An earlier study in the same study area (Reitalu *et al.* 2009) showed that fine-scale species diversity was associated with both present and past habitat factors. Associations between current species diversity and past habitat conditions have been explained by the time-lag that may exist between the changes in habitat conditions and the community-level response to these changes (Ernoult *et al.* 2006; Helm *et al.* 2006; Metzger *et al.* 2009). Changes in species diversity are expected to be an outcome of filtering processes that select for species that have specific sets of traits (Mayfield *et al.* 2010).

The present study reveals quantitative links between present-day functional trait composition of grassland communities and both present and past habitat conditions. Our results suggest that the present-day distribution of the measured functional traits represents a legacy from historical filtering on the set of species available at a given site (Diaz *et al.* 2007b; Mayfield *et al.* 2010). The significant associations between present-day functional composition and historical factors (Table 2) indicate that the functional response of plant communities may exhibit a relatively long time-lag in relation to changes in habitat conditions. This delayed response of functional trait composition to environmental change reinforces the view that both past and present biodiversity drivers need to be taken into account in the development of reliable indicators of biodiversity change – especially in semi-natural grasslands (Bruun *et al.* 2001; Lindborg & Eriksson 2004; Helm *et al.* 2006; de Bello *et al.* 2010).

Present grazing intensity

Grazing intensity was the most important variable influencing both CWM and FD in the present study (Table 2), and our results suggest that grazing favours the coexistence of species that differ in their reproductive and persistence traits. Continued abandonment of grazing management in the present-day landscape will be likely to result in a loss of functional trait diversity in seed mass, leaf size, reproductive height (natural) and lateral spread, and consequently lead to the loss of potential ecosystem functions associated with those traits and to a long-term negative effect on species diversity (see Garnier *et al.* 2007; Mayfield *et al.* 2010).

Grazing was associated with a decrease in the CWM but an increase in the FD of the natural reproductive height, suggesting that the mean vegetative height (CWM) alone is not sufficient as an indicator of grazing intensity (Klimesova *et al.* 2009). McIntyre *et al.* (1999) suggested that a combination of reproductive and vegetative height could be used to assess exposure of reproductive structures to vertebrate herbivores. While high grazing intensity was associated with reduced average plant height in the present study, grazing may also promote the coexistence of species with different heights at low grazing intensity (e.g. Louault *et al.* 2005).

Table 1. Measured traits, their functional significance and related publications.

	Unit	Definition	Associated with	References
Whole plant traits (no. seedlings)				
Canopy height	cm	natural and stretched distance between the highest photosynthetic tissue and the ground	competitive ability	Weiher et al., 1999; Westoby et al., 2002
Reproductive height	cm	natural and stretched distance between the highest dispersal unit and the ground	dispersal ability	Van der Pijl 1972
Lateral spread	cm	the space occupied by the plant if projected onto the ground	competitive ability persistence	Klimes & Klimesova 2000; Vesk & Westoby 2004
Leaf traits (fully mature current-year leaves (method described by Garnier et al., 2001))				
Leaf size	mm^2	area of one side of a fresh leaf	growth rate competitive ability stress tolerance	Westoby et al., 2002; Kleyer et al., 2008
Toughness	$kg\ cm^{-1}$	calculated as the force needed to tear a leaf along its longest axis, divided by the leaf width (measured using an apparatus specially designed for the purpose)	growth rate disturbance tolerance persistence	Cornelissen et al., 2003; Kitajima & Poorter, 2010
SLA	$mm^2\ mg^{-1}$	Specific leaf area: the ratio of fresh leaf area to leaf dry mass	growth rate	Cornelissen et al., 2003
LDMC	$mg\ g^{-1}$	Leaf dry matter content: the ratio of dry leaf mass to fresh leaf mass	growth rate competitive ability	Westoby et al., 2002; Kleyer et al., 2008
Seed traits (5 to 15 individuals per species)				
Seed mass	mg	mean mass of ten air dried dispersules	dispersal competitive ability establishment	Grime et al., 1998; Westoby et al., 2002

Table 2. Minimal adequate regression models (simultaneous autoregressive models, SAR_{error}) of the relationship between the measures of functional structure and environmental variables. Signs indicate positive (+) or negative (-) regression coefficients. +++/--- $P \leq 0.001$, ++/-- $P \leq 0.01$, +/- $P \leq 0.05$.

	Grazing	Shrub	Tree	Age	% Grassland				% Forest		
		cover	cover		2004	1938	1835	1800	2004	1938	1835
Functional divergence											
Natural canopy height		++									
Stretched canopy height	--				--					---	---
Natural reproductive height	+++					+					--
Stretched reproductive height	--										
Lateral spread	+++					+++					
Leaf size	+++			+							
SLA				+++							
LDMC						--					
Toughness			-					+++			
Seed mass	++	+									-
Community weighted mean											
Natural canopy height	---							--			
Stretched canopy height	---							---			
Natural reproductive height	---							---			
Stretched reproductive height	---							---			
Lateral spread		++			--				--		
Leaf size		+++						---			
SLA		---								+++	--
LDMC	---		++					--			
Toughness	---	--									
Seed mass											

Leaf size is considered to be a good predictor of response to environmental stresses (Cornelissen *et al.* 2003), such as grazing disturbance. The relationship between grazing and leaf size might, therefore, be expected to depend on the time and duration of the disturbance, with long term grazing management leading to a community with small-leaved species (Dìaz *et al.* 2001). However, in our study grazing showed a significant association with the FD of leaf size but was not associated with the CWM of leaf size.

Both mean leaf toughness and mean LDMC decreased with grazing intensity, indicating that dominant species in the grassland community have tougher leaves in ungrazed sites than in more heavily grazed sites, as has been shown in earlier studies (Cingolani *et al.* 2007; Quétier *et al.* 2007).

Landscape context, habitat structure and grazing continuity

The within-patch cover of woody species (shrubs and trees), and the current percentage of grassland and forest in the surroundings of the plots are both variables that may have indirect effects on the fine-scale composition of the species and traits in grassland vegetation. Woody cover is expected to reflect the management status over a relatively long time period (Reitalu *et al.* 2009). Shrub cover may also be positively associated with heterogeneity in light conditions in the surrounding of the plots. The greater the proportion of woody vegetation in the surroundings, the more the assemblage of trait values may be expected to reflect an advanced stage of succession/abandonment (cf. Kahmen & Poschlod 2004). Our results are consistent with this expectation, with a significant increase in CWM leaf size and CWM lateral spread with increasing percentages of shrub cover within the grassland patches (Table 2). In general, the present-day vegetation surrounding the plots may be expected to have an impact on plant functional structure within grassland communities because of the importance of the local species pool (*sensu* Zobel (1997)) for recruitment.

The percentage of grassland surrounding the plots in the oldest time period (1800) was the second most important variable, after grazing intensity, in explaining the overall trait composition. Reitalu *et al.* (2009) suggested that the positive associations between the proportion of grassland in 1800 and present-day species diversity variables, in both old and young grasslands in the same study area, indicate that the development and persistence of a species-rich grassland flora is favoured in areas that are, or have historically been, surrounded by old grasslands. The present results indicate that the plots that were surrounded by high proportions of grassland in 1800 are not only taxonomically more diverse than historically isolated grasslands but also more diverse functionally.

Apart from the FD in SLA and leaf size, we found no significant effects of the age of the grasslands on their functional trait composition (Table 2). The historical percentage of grasslands in the surroundings is a better predictor of present-day functional composition than the management continuity of the individual grassland sites. The functional composition in grassland patches in the fragmented present-day landscape still reflects their context within a vanished landscape – where the presence of extensive grasslands in the immediate surroundings gave access to a diverse pool of grazing-tolerant species.

Conclusions

The present day functional trait composition of grassland communities reflects ecological and demographic processes that are, and have been, operating both in the present and past landscape. As a consequence, attempts to explain present functional trait composition solely in terms of current habitat conditions provide a limited perspective on the driving forces behind the maintenance or loss of biodiversity. The present study illustrates the ways in which information on current grazing intensity, the local species pool, and on land-use history can help to explain the trait composition in semi-natural grassland communities within the modern landscape. Our study is, as far as we know, the first to establish quantitative relationships between functional trait composition and historical properties of the landscape, and suggests that there is likely to be a time lag in the response of ecosystem functioning to environmental change.

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Supplementary material

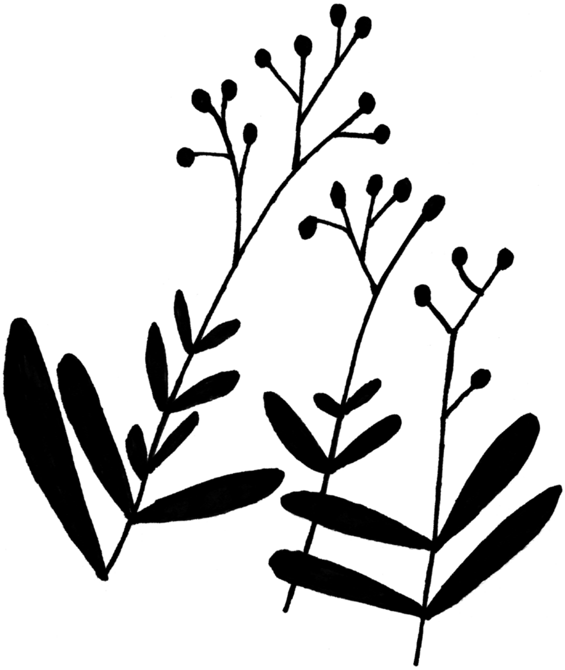
Appendix 1. Dominant and subdominant species (n=61). The family, lifespan (annual “a”, biennial “b” or perennial “p”), life form (grass “g”, forb “f” and/or legume “l”), mean relative abundance (%) and frequency of occurrence in plots (%) are given for each species. Nomenclature follows Mossberg & Stenberg (2003).

Species (taxon)	Family	Lifespan	Life form	Abundance	Frequency
Achillea millefolium	Asteraceae	p	f	2.28	59.77
Agrostis capillaris	Poaceae	p	g	3.02	56.87
Agrostis vinealis	Poaceae	p	g	2.03	44.68
Alchemilla sp.	Rosaceae	p	f	0.04	2.71
Anemone pratensis	Ranunculaceae	p	f	0.52	30.56
Anthoxanthum odoratum	Poaceae	p	g	1.12	29.01
Anthyllis vulneraria	Fabaceae	b/p	f/l	1.25	43.13
Arabis hirsuta	Brassicaceae	p	f	0.17	13.93
Arenaria serpyllifolia	Caryophyllaceae	a	f	0.95	31.33
Arrhenatherum elatius	Poaceae	p	g	0.24	14.31
Asperula tinctoria	Rubiaceae	p	f	0.89	22.24
Briza media	Poaceae	p	g	3.04	60.74
Bromus hordeaceus	Poaceae	p	g	0.95	22.05
Campanula persicifolia	Campanulaceae	p	f	0.33	10.06
Campanula rotundifolia	Campanulaceae	p	f	0.98	26.69
Carex caryophyllea	Cyperaceae	p	g	0.25	23.98
Carex caryophyllea/ericetorum	Cyperaceae	p	g	2.48	54.35
Carex ericetorum	Cyperaceae	p	g	0.08	7.54
Centaurea jacea	Asteraceae	p	f	1.01	33.08
Cerastium fontanum	Caryophyllaceae	p	f	1.77	58.03
Cynosurus cristatus	Poaceae	p	g	0.58	19.92
Dactylis glomerata	Poaceae	p	g	0.32	23.02
Festuca ovina	Poaceae	p	g	8.70	98.45
Filipendula vulgaris	Rosaceae	p	f	3.38	51.64
Fragaria vesca/viridis	Rosaceae	p	f	4.24	0.00
Galium boreale	Rubiaceae	p	f	0.94	20.70
Galium verum	Rubiaceae	p	f	5.79	88.97
Helianthemum nummularium	Cistaceae	p	f	2.84	49.71
Helianthemum oelandicum	Cistaceae	p	f	0.24	7.93
Helictotrichon pratense	Poaceae	p	g	3.90	60.74
Helictotrichon pubescens	Poaceae	p	g	1.54	43.71
Hypericum perforatum	Clusiaceae	p	f	0.25	15.67
Linum catharticum	Linaceae	a	f	1.76	45.84

Species (taxon)	Family	Lifespan	Life form	Abundance	Frequency
Lotus corniculatus	Fabaceae	p	f/l	0.85	40.43
Luzula campestris	Juncaceae	p	f	3.00	70.79
Medicago sativa ssp. falcata	Fabaceae	p	f/l	1.53	31.33
Medicago lupulina	Fabaceae	p	f/l	1.94	50.87
Melampyrum cristatum	Scrophulariaceae	a	f	0.07	4.84
Oxytropis campestris	Fabaceae	p	f/l	0.10	4.26
Phleum phleoides	Poaceae	p	g	1.84	45.65
Pilosella officinarum	Asteraceae	p	f	2.03	50.68
Plantago lanceolata	Plantaginaceae	p	f	3.70	88.59
Poa pratensis ssp. angustifolia	Poaceae	p	g	2.59	65.57
Potentilla argentea	Rosaceae	p	f	0.26	14.51
Potentilla reptans	Rosaceae	p	f	0.25	7.16
Potentilla tabernaemontani	Rosaceae	p	f	2.99	75.63
Prunella grandiflora	Lamiaceae	p	f	0.22	8.70
Ranunculus bulbosus	Ranunculaceae	p	f	3.91	89.75
Rumex acetosa	Polygonaceae	p	f	0.13	7.54
Rumex acetosella	Polygonaceae	p	f	0.10	3.29
Sanguisorba minor	Rosaceae	p	f	0.14	5.22
Satureja acinos	Lamiaceae	a	f	0.29	11.41
Saxifraga granulata	Saxifragaceae	p	f	0.30	15.47
Sedum acre	Crassulaceae	p	f	0.65	20.12
Silene nutans	Caryophyllaceae	p	f	0.05	3.29
Taraxacum sect. Erythrosperma	Asteraceae	p	f	0.57	39.07
Thymus serpyllum	Lamiaceae	p	f	0.79	23.40
Trifolium arvense	Fabaceae	a	f/l	0.10	8.12
Trifolium pratense	Fabaceae	p	f/l	0.46	18.96
Veronica chamaedrys	Scrophulariaceae	p	f	0.18	7.74
Veronica spicata	Scrophulariaceae	p	f	1.24	31.53
Viola hirta	Violaceae	p	f	0.32	24.76

Appendix 2. Pearson’s product-moment correlations (r) between the explanatory variables.
*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

		% Grassland				% Forest				Tree cover	Shrub cover
		2004	1938	1835	1800	2004	1938	1835	Age		
% Grassland	1938	0.29***									
	1835	0.06	0.10*								
	1800	-0.08	0.55***	0.53***							
% Forest	2004	-0.49***	0.43***	0.27***	0.64***						
	1938	-0.18***	-0.16***	0.57***	0.39***	0.52***					
	1835	-0.16***	0.53***	-0.54***	0.22***	0.47***	-0.19***				
Age		0.04	0.20***	0.43***	0.40***	0.16***	0.17***	-0.19***			
Tree Cover		-0.02	-0.24***	-0.09	-0.18***	-0.15***	0.05	-0.11*	-0.08		
Shrub cover		-0.04	0.03	-0.18***	-0.05	0.07	0.01	0.15**	-0.16***	0.25***	
Grazing		0.16***	0.07	0.22***	0.08	-0.13**	-0.11*	-0.15***	0.22***	-0.15**	-0.55***



V Temporal changes in biodiversity

Contrasting changes in taxonomic, phylogenetic and functional diversity during secondary grassland succession

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Abstract

A better understanding of the processes that generate biodiversity during succession will allow more realistic predictions about ecosystem responses to disturbance. Comparative analysis of taxonomic, phylogenetic and functional diversity represents a powerful method for exploring community assembly processes, but studies of successional dynamics have yet to integrate the analysis of these three aspects of biodiversity and their spatial turnover (beta diversity).

In the present study, taxonomic, phylogenetic and functional (alpha and beta) diversity were estimated for four stages within a more than 300 year long chronosequence, representing an arable-to-grassland succession, using a dated phylogeny and a set of eleven plant functional traits. The extent to which the phylogenetic and functional similarity of species (both within and between communities) differed from random expectations, given the taxonomic diversity, was assessed for each successional stage.

Integrated analysis of taxonomic, phylogenetic and functional diversity provided new insights into the processes that contribute to changes in grassland biodiversity after disturbance. The three aspects of diversity showed contrasting overall patterns of temporal change during succession, with significant increases in functional and phylogenetic alpha diversity between the mid and the final successional stages that were not accompanied by a change in species richness. A long continuity of grazing management promotes functional and phylogenetic diversity: functionally similar and closely related species in the early and mid successional stages are replaced by functionally and phylogenetically more unique species in the old grasslands. Species were functionally more similar than expected within the first three successional stages, suggesting that environmental filtering and dispersal limitation play an important role in community assembly during early and mid succession. Functional beta diversity decreased over time – more rapidly than would be expected given the taxonomic beta diversity, indicating that changes in community composition during succession are driven by non-random processes.

Keywords: alpha diversity, beta diversity, semi-natural grasslands, chronosequence, trait, environmental filtering, functional diversity, phylogenetic diversity, taxonomic diversity, dispersal

Introduction

The world's ecosystems are becoming increasingly modified by human activities, and an understanding of the processes that generate and maintain biodiversity during succession following disturbance is essential for predictions about ecosystem responses to future environmental change (Connell & Slatyer 1977; Noble & Gitay 1996; Loreau et al. 2003; Isbell et al. 2011; Prach & Walker 2011). The process of community assembly during succession may be driven by both stochastic and deterministic processes (Huston & Smith 1987). Deterministic processes include biotic and abiotic filtering which, together or in combination, select for species with specific sets of traits (e.g. Keddy 1992; Zobel 1997; Götzenberger et al. 2011; Weiher et al. 2011). Theory predicts that the relative importance of these assembly processes is likely to change as succession proceeds, with dispersal limitation and environmental filtering dominating during early succession and competition becoming increasingly important in the later stages of succession (Connell & Slatyer 1977; Leibold et al. 2004).

Earlier studies of community assembly during succession have mainly focussed on temporal changes in taxonomic composition, on changes in single traits, or on changes in functional groups (Noble & Slayter 1980; Prach et al. 1997; Garnier et al. 2004; Kahmen & Poschlod 2004). The fact that these studies do not take into account the multivariate correlations between traits, or allow for the possibility that species within functional groups may be functionally different, causes bias in the detection of the underlying assembly processes (Cornwell et al. 2006; Villéger et al. 2008).

Recently developed methods that test whether the functional trait and phylogenetic diversity within communities (alpha diversity) and/or functional and phylogenetic turnover between communities (beta diversity) is higher or lower than expected from a random draw of species from the species pool (Webb 2000; Webb et al. 2002) provide a potentially more powerful approach to the detection of assembly processes. In trait-based approaches, a lower than expected functional alpha diversity indicates that the species co-occurring in local communities are more similar than would be expected by chance (functional clustering), because of environmental filtering and/or trait-based dispersal limitation. A higher than expected functional alpha diversity indicates that the species in a local community are less similar than expected (functional overdispersion), which would be a predicted consequence of competitive exclusion of functionally similar species. A higher than expected functional turnover between communities (beta diversity) indicates that communities are functionally more dissimilar than expected, given the taxonomic turnover, because of the filtering effect of an underlying environmental gradient and/or dispersal limitation (Stegen & Hurlbert 2011; Swenson 2011). Because functional diversity measures are based on a finite set of traits, phylogenetic diversity is often used as a proxy for functional trait diversity (see Webb 2000; Webb et al. 2002; Cadotte et al. 2009), as it potentially integrates a greater amount of trait information than is provided by a limited set of measurable traits. However, inferences about community assembly processes based on phylogenetic diversity rely on the assumption of trait conservatism, the expectation that closely related species will be ecologically similar (Wiens & Graham 2005). A mismatch between functional and phylogenetic diversity would indicate that the phylogenetic diversity does not reflect the diversity of phylogenetically conserved traits and/or that important traits were missing from the analysis (Pavoine & Bonsall 2010). Simultaneous analysis of functional and phylogenetic diversity may therefore provide more realistic insights into community assembly processes than the consideration of a single aspect of diversity.

A few studies have quantified either functional or phylogenetic diversity at different stages during succession. Studies of changes in phylogenetic alpha diversity during tropical forest succession have shown that late successional communities contain less closely related species than early successional communities (Letcher 2010; Norden et al. 2011), and the study by Fukami et al. (2005) revealed that functional beta diversity in experimental grassland plant communities declined (functional convergence) over succession, more steeply than expected given the taxonomic beta diversity.

In the present study, we assessed taxonomic, phylogenetic and functional (alpha and beta) diversity, at four stages during a more than 300 year long arable to semi-natural grassland succession. Semi-natural grasslands are among the most diverse plant communities within the European agricultural landscape and have developed as result of a long history of low-intensity grazing management, and without the use of artificial fertilizers (Eriksson et al. 2002; Poschlod & WallisDeVries 2002).

First, we quantified taxonomic, phylogenetic and functional diversity within grassland communities (alpha diversity), together with the taxonomic, phylogenetic and functional turnover between communities (beta diversity), within each of the four successional time steps (using detailed phylogenetic information as well as a set of eleven plant functional traits, derived from recent trait data bases (Poschlod et al. 2003; Kleyer et al. 2008)). If changes in environmental conditions during succession affect community assembly processes, rather than the species diversity *per se* (Mayfield et al. 2010), temporal changes in functional and phylogenetic diversity are expected to differ from changes in taxonomic diversity.

Second, we tested whether phylogenetic and functional (alpha and beta) diversity within each of the successional time steps is higher or lower than expected, given the taxonomic diversity. If environmental filtering and dispersal limitation play an important role in community assembly during early and mid succession (Connell & Slatyer 1977), species within the first successional stages should be more closely related and functionally and phylogenetically more similar (i.e. have a lower alpha diversity) than expected given the observed species richness. If community assembly throughout succession is deterministic, both functional and phylogenetic beta diversity are expected to decrease over time – more rapidly than expected given the taxonomic beta diversity (Fukami et al. 2005; Swenson et al. 2011). If the traits that were used to estimate functional diversity are phylogenetically conserved, then functional and phylogenetic diversity will be expected to show similar patterns of deviation from random expectations.

Materials and methods

Study area and sampling

We studied grassland plant communities in a chronosequence representing an arable to semi-natural grassland succession within a 4.5 × 4.5 km landscape on the Baltic Island of Öland (centred on 56°40’49’’ N, 16°33’58’’ E). The overall topography in the study area is flat and the landscape consists of a mosaic of grasslands, arable fields and forests. Öland has a history of grazing management that dates back until the early Neolithic (3900-3300 BC), but the proportion of grassland in the study area has declined progressively over the last three centuries – from 86% in 1723 to 9% at the present-day (Johansson et al. 2008). The remaining grassland fragments are still grazed extensively, by free-ranging cattle, and younger grasslands have also developed on previously arable fields (Johansson et al. 2008).

Vegetation surveys were carried out in old semi-natural grasslands and in younger grasslands on previously arable sites. The grasslands were assigned to four successional stages (early, early-mid, late-mid and late succession), corresponding to 5-15, 16-50, 51-270 and ≥270 years of grassland continuity, using GIS-overlay analysis based on historical land use maps (Johansson et al. 2008). Presence/absence data were collected for all non-woody, vascular plant species (234 in total) within 2 × 2 m plots (local communities), between mid-May and mid-July 2009. Each of the four successional stages is represented by 55 plots (n=220 in total).

Within each plot, mixed soil samples (3-5 per plot), from the upper 7.5 cm of the soil, were collected and stored at -18°C until analysis. Plant available phosphorus was estimated using the Bray 1 method. Within each plot, the amount of disturbance was characterized by the percentage of bare ground.

Trait data

We used eleven plant functional traits that are associated with species' response and/or resistance to disturbance (Fig. A1 in Supplementary Material). All traits were compiled/derived from large data bases for the North-West European Flora (Poschlod et al. 2003; Kleyer et al. 2008). The total set of traits consisted of (a) five vegetative traits (canopy height, plant life form, specific leaf area (SLA), leaf size, leaf dry matter content (LDMC)), mainly related to the plant species' competitive ability, growth rate and the ability to respond to environmental stress; and (b) six regenerative traits (epizoochory, wind dispersal potential, adult plant longevity, seed bank persistence, seed mass, seed production per ramet) related to species' ability to disperse in space and time. Qualitative data on plant life form were coded as a quantitative variable (cryptophytes and therophytes = 1, hemicryptophytes = 2, chamaephytes = 3 and phanerophytes = 4 (cf. Pakeman et al. 2011). Wind dispersal potential, on an ordinal scale, was derived from data on seed terminal velocity and seed release height (Tackenberg et al. 2003); epizoochorous dispersal potential was predicted from seed mass and seed morphology using the regression model proposed by Römermann et al. (2005). Adult plant longevity was inferred from data on plant life span and on clonal propagation, using three ordinal classes "annual and biennial", "perennial/without the ability to spread clonally", and "perennial showing clonality". Seed bank persistence was characterized by the longevity index (Thompson et al. 1997; Bekker et al. 1998).

Because data for all eleven traits were not available for the full set of species, estimates for missing values (9.1% of the cases) were obtained by predictive mean matching based on the observed trait values, using multivariate imputation by chained equations (MICE) as implemented in the package 'mice' (van Buuren & Groothuis-Oudshoorn 2011) in the R statistical package (R Development Core Team 2011). MICE uses Gibbs-sampling and, for each trait, the robustness of the imputation procedure could be verified by the observation that the Gibbs sampler for five imputation runs converged within less than 100 iterations.

Phylogeny

For the 234 species in our study, we constructed a phylogenetic tree ('regional supertree'), based on a published supertree for Central European angiosperms without branch length information (Durka 2002; with updated topology). Internal nodes of the supertree were dated with the help of an extensive literature survey on published ages of the respective branching events. An ultrametric tree was created by distributing nodes without dating information evenly between dated nodes using the 'bladj' algorithm of Phylocom (Webb et al. 2008). Species that were not included in the supertree (*Helianthemum oelandicum, Oxytropis campestris, Ranunculus auricomus, Sesleria uliginosa)* were added manually. The final tree included 218 internal nodes of which 12 (6 %) were polytomies. All polytomies were below the family level, with seven (58 %) at the generic level (Fig. A1 in Supplementary Material).

Analysis

Within each of the four successional stages we calculated measures of taxonomic, phylogenetic and functional alpha and beta diversity, in order to (a) assess the way in which taxonomic, phylogenetic and functional diversity changes during succession and (b) quantify the extent to which the observed patterns of phylogenetic and functional diversity differ from random expectations, given the species (taxonomic) diversity. For consistency, the functional and phylogenetic diversity indices were calculated using identical methods within the R-package 'picante' (Kembel et al. 2010)

Within-community (alpha) diversity

Taxonomic diversity (*Tax_Alpha*) was assessed using species richness. Phylogenetic and functional alpha diversity (*Phyl_Alpha, Funct_Alpha*) were assessed using the mean pairwise distance (MPD), a measure of the average and phylogenetic and functional relatedness of the species that co-occur in a local community. For each community, phylogenetic alpha diversity, the average branch length between species in a local community, was calculated from a phylogenetic 'cophenetic' distance matrix. Functional alpha diversity was obtained from a species distance matrix based on the eleven functional traits. Because some of the traits in the study were highly correlated and likely to dominate the distance matrix, although they represent similar aspects of plant functional differentiation (cf. Swenson & Enquist 2009), we carried out principal component analysis (PCA) on the log-transformed and standardized (mean=0, SD=1) trait data (Devictor et al. 2010; Swenson et al. 2011). The resulting PCA axes were used to construct the inter-species functional distance matrix from which the mean pairwise distance (*Funct_Alpha*) for each community was calculated. *Funct_Alpha* represents a composite measure of functional similarity between species in a local community.

In order to assess whether the phylogenetic and functional relatedness, between the species in the local communities, within each of the four successional time steps, is lower or higher than expected from a random draw of species from the regional species pool (N=234), we compared the observed alpha diversity values with the alpha diversity values from 999 random communities. Random communities were generated by shuffling the species names on the functional and phylogenetic distance matrix, thereby maintaining (a) the species richness of each community, (b) the occurrence frequency of the species across the landscape, (c) the patterns of spatial clustering (e.g. caused by dispersal limitation) and (d) the species identity within each time step. This null model is more appropriate for the comparison of alpha diversity between successional time steps than null models (e.g. swap algorithms) that randomize within the species-by-plot (community) matrix and which would neither maintain the species identity within each time step nor the observed patterns of dispersal limitation (Hardy 2008; Norden et al. 2011). For each community, the standardized effect size (*Alpha_Stand*) was calculated according to Gotelli & Rohde (2002) as the observed phylogenetic and functional alpha diversity relative to the alpha diversity of the 999 random communities: *Alpha_Stand = (Alpha - Alpha_Rand)/SD_Alpha_Rand,* where *Alpha* is the observed alpha diversity value in a local community, *Alpha_Rand* the mean and *SD_Alpha_Rand* the standard deviation of alpha diversity values obtained from the 999 random communities. Negative *Alpha_Stand* values indicate that species in a local community are functionally or phylogenetically, more similar than expected by chance. Positive *Alpha_Stand* values indicate that species that co-occur in a local community are less related than expected by chance. Significant deviations from random expectation occur if *Alpha_Stand* values are less than -2 or greater than 2.

Differences in alpha diversity between the four successional time steps were assessed with ANOVA and Tukey's HSD post-hoc tests, accounting for unequal variances and using the false discovery rate (Benjamini & Yekutieli 2001) for p-value corrections, within the R-packages 'multcomp' (Hothorn et al. 2008) and 'sandwich' (Zeileis 2004).

Between-community (beta) diversity

In addition to taxonomic, phylogenetic and functional diversity within local communities, we also quantified the taxonomic, phylogenetic and functional distance between communities (beta diversity).

Taxonomic beta diversity (*Tax_Beta*) was calculated using the Sørenson index in the R-package 'vegan' (Oksanen et al. 2011).

Both phylogenetic and functional beta diversity were assessed using indices analogous to the traditional Sørensen similarity index and defined as the fraction of branch length, in a phylogenetic tree (see PhyloSor index in Bryant et al. 2008) or a functional trait dendrogram (see FSor index in Swenson et al. 2011), that is shared between two communities. In our study, beta diversity (*Phyl_Beta, Funct_Beta*) was expressed as dissimilarity (1-PhyloSor, 1-FSor) and calculated between all communities within each of the four successional time steps. Calculations of phylogenetic beta diversity were based on the 'regional' phylogenetic supertree. Functional beta diversity was obtained from a functional dendrogram that was constructed using UPGMA clustering (Petchey & Gaston 2002) on the species distance matrix which was used to calculate functional alpha diversity. Functional and phylogenetic beta diversity ranges between 0 (two communities are composed of the same taxa) and 1 (both communities have no taxa in common).

To test whether two communities are phylogenetically or functionally more or less dissimilar than expected given the taxonomic beta diversity, we compared the observed beta diversity values with a null distribution of beta diversity values, that was generated by shuffling (999 times) the species names on the phylogenetic or functional tree. This null model randomizes the dissimilarities within the phylogenetic and functional distance matrix, equivalent to the null-model that was used for alpha diversity, and therefore maintains the number of species shared between communities (Bryant et al. 2008). A standardized effect size (*Beta_Stand*) was calculated, from the observed beta diversity and the mean and the standard deviation of the simulated beta diversity values (see *Alpha_Stand*). Positive *Beta_Stand* values greater than 2, indicate that the phylogenetic or functional dissimilarity between communities is higher than expected given the species beta diversity, negative *Beta_Stand* less than -2 indicate the communities are phylogenetically or functionally more similar than expected from random.

Differences in mean beta diversity between the four successional age classes were assessed using ANOVA and pairwise comparisons. Because the values within the dissimilarity matrices are not independent of each other, P-values were obtained using non-parametric permutation testing (R-package 'lmPerm' (Wheeler 2010)).

Phylogenetic signal

To assess the extent to which the phylogenetic relatedness between species reflects ecological similarity (i.e. phylogenetic conservatism), we used Blomberg's K-statistic (Blomberg et al. 2003) to quantify the phylogenetic signal in each of the eleven traits in the regional phylogenetic supertree (R-package 'phytools' (Revell 2011)). K-values greater than one indicate significant phylogenetic signal. K-values close to zero indicate weak phylogenetic signal, implying that closely related species are ecologically distinct.

Results

Alpha diversity

All three components (taxonomic, phylogenetic and functional) of alpha diversity increased over succession but showed different temporal patterns (Fig.1). Taxonomic alpha diversity (species richness) increased asymptotically over time, with significant increases between early and late-mid succession (5-270 years), but no further increase in the last successional time step (> 270 years). In contrast, there was no significant increase in phylogenetic or functional diversity between the early and early-mid successional stages (5-50 years). Instead, functional and phylogenetic diversity increased steeply between the second and the fourth (last) successional time step, reaching their highest levels in the oldest grassland.

Functional and phylogenetic alpha diversity were significantly, positively correlated with species richness ($r = 0.49$, $P < 0.001$ and $r = 0.43$, $P < 0.001$, see Table A2 in Supplementary Material). In order to determine whether the observed patterns of functional and phylogenetic alpha diversity were lower or higher than expected, given the species richness, we carried out null model analysis. The standardized values for phylogenetic and functional diversity (*Alpha_Stand*) were consistently negative (phylogenetically and functionally clustered) within all successional time steps, and were lowest in the early and mid successional stages (5-270 years; Fig. 2).

However, significant clustering (with *Alpha_Stand* values < 2) was only detected for functional diversity, indicating that species in early and mid successional communities were functionally more similar than expected, given the species richness. Phylogenetic alpha diversity was not significantly different from null expectations in any of the successional time steps but showed a temporal trend, with early successional communities containing more closely related species than the communities within the latest successional stage.

Beta diversity

All three components (taxonomic, phylogenetic and functional) of beta diversity decreased from the early to late successional stages (Fig.3).

The measures of functional and phylogenetic beta diversity were both significantly, positively correlated with taxonomic beta diversity ($rM = 0.981$, $P < 0.001$ and $rM = 0.858$, $P < 0.001$, see Tab. A3 in Supplementary Material). Standardized effect sizes for functional and phylogenetic beta diversity (*Beta_Stand*) were consistently positive across the four successional time steps, indicating that the phylogenetic and functional turnover within each of the successional stages is higher than expected, given the taxonomic turnover (Fig. 4).

Beta_Phyl_Stand and *Beta_Funct_Stand* values were less than 2 in all the successional time steps, but the standardized effect sizes for phylogenetic and functional diversity showed opposing temporal patterns. Whereas *Beta_Funct_Stand* was highest within the first successional stages and decreased towards values close to the null expectation in the last successional time step, *Beta_Phyl_Stand* increased between the first and the third successional time steps.

Discussion

Simultaneous analysis of taxonomic, phylogenetic and functional diversity represents a potentially powerful tool for the study of the temporal dynamics of the processes that generate biodiversity after disturbance (Letcher 2010; Pavoine & Bonsall 2011). Our study demonstrates that taxonomic, phylogenetic and functional (alpha and beta) diversity show non-congruent patterns of change

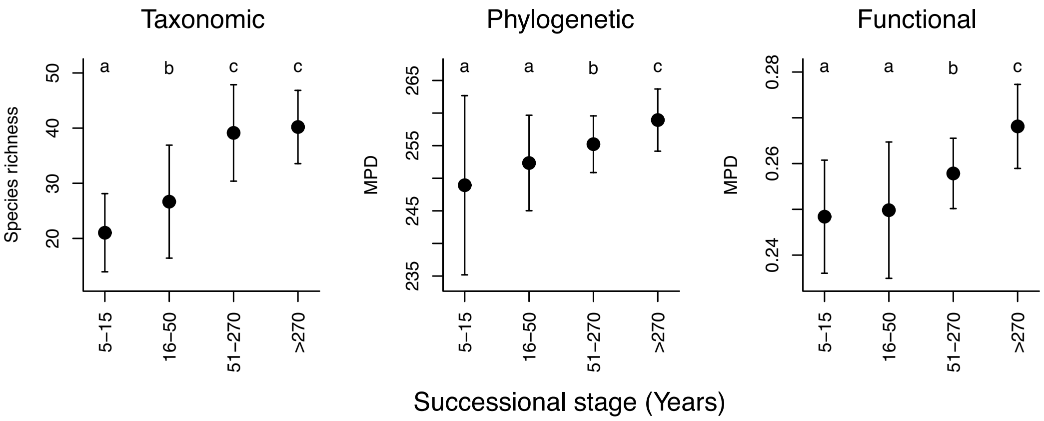

Fig. 1. Taxonomic, phylogenetic and functional alpha diversity (mean ± 1 SD) within the four successional age classes. Phylogenetic and functional alpha diversity are represented by the mean pairwise distance (MPD). Letters indicate significant differences between the successional timesteps.

during succession. Although there were no changes in species richness between the mid and late successional stages, there was a significant increase in phylogenetic and functional alpha diversity – long grazing continuity promotes functional and phylogenetic diversity. Species within early to mid successional communities were functionally more similar than expected, given the species diversity. Trait-based environmental filtering and dispersal limitation appear to play a more important role in shaping grassland plant communities within the early to mid succession than within the late successional stages.

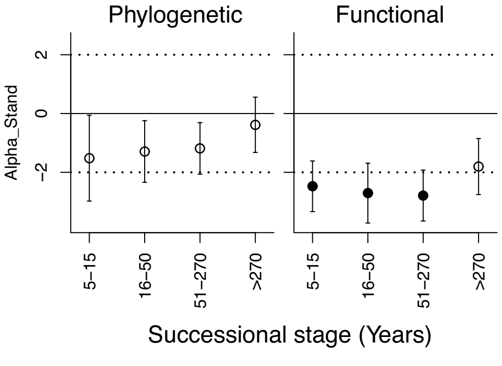

Fig. 2. Standardized effect sizes of phylogenetic and functional alpha diversity (mean ± 1 SD). Values < 0 indicate that phylogenetic or functional alpha diversity is lower than expected, given the species richness. The dotted lines indicate the 0.05 significance levels. Values < -2 (black dots below the lower dotted line) indicate that functional diversity is significantly lower than expected (functional clustering).

Alpha diversity

Taxonomic, phylogenetic and functional alpha diversity all increased during succession but showed different temporal patterns, suggesting that these three facets of within-community diversity provide complementary measures of changes in biodiversity during succession (Fig. 1). The number of species increased between the early and early-mid successional time steps. However, the absence of significant increases in functional or phylogenetic alpha diversity indicates that the increase in species richness between the early and mid successional stages mainly represents the entry of closely related, and functionally similar, species. In contrast, there were no significant changes in species richness between the late-mid and the last successional time step. However, despite the lack of change in the number of species, significant increases in functional and

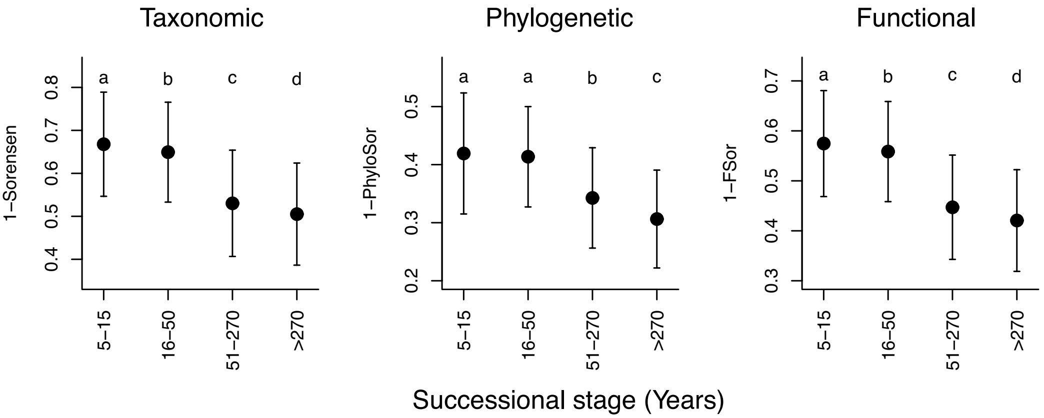

Fig. 3. Beta diversity (mean ± 1 SD), based on Sørensen's index, within the four successional age classes. Beta diversity value are expressed as dissimilarities. Letters indicate significant differences between the successional timesteps.

phylogenetic diversity reveal that closely related and/or functionally similar species are replaced by functionally and phylogenetically more distinct species between the late-mid and late successional stages.

Both functional and phylogenetic alpha diversity were lower than expected (given the observed levels of species richness) throughout the arable-to-grassland succession (Fig. 2), suggesting that the assembly of species into local communities and the observed changes in diversity are governed by non-random processes. However, significant deviations from random expectations were only detected for functional diversity in early and mid succession. The fact that communities within the early and early-mid successional time steps contained more functionally similar species than predicted by chance may be explained by trait-based dispersal filtering that favoured species with high long-distance dispersal potential (Fig. 5), and/or by the effects of strong environmental filtering (Dinnage 2009; Helmus et al. 2010).

Effects of large-scale disturbance and fertilization during arable cultivation have been shown to persist during the early stages of subsequent arable-to-grassland successions (Fraterrigo et al. 2005; Carbajo et al. 2011; Ceulemans et al. 2011), and the habitats of the early and mid successional communities in the present study were characterized by a high proportion of bare soil and high levels of total phosphorus (Fig. 6).

Agricultural disturbance is likely to have acted as environmental filter, that has selected for fast growing and stress-tolerant species that produce

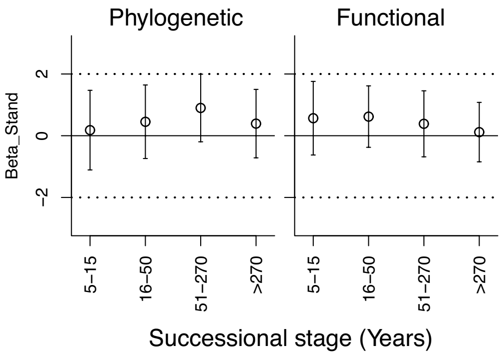

Fig. 4. Standardized effect sizes of beta diversity (mean ± 1 SD). Values > 0 indicate that the phylogenetic or functional beta diversity is higher than expected, given the species beta diversity. Values > 2, above the dotted line, indicate a significantly higher than expected phylogenetic or functional turnover.

large numbers of seeds (high SLA, canopy height and high seed production (see Fig. 5; Marrs 1993; cf. Dinnage 2009)). At the same time, lower levels of interspecific competition in the less dense vegetation of the early and early-mid successional habitats may allow the co-existence of functionally similar species (cf. Dinnage 2009; Pakeman 2011). Our finding that the species occurring in the old (late successional) grasslands appear to be less functionally similar than in the early successional communities suggests that, as succession proceeds, the relative importance of environmental filtering and dispersal limitation decreases. Competitive exclusion of functionally similar species (MacArthur & Levins 1967; Grime 2006) may play a stronger role in community assembly as the grass sward becomes more dense and resources, such as phosphorus, become limiting in the old grasslands (Fig. 6; see Lambers et al. 2008). The high levels of functional diversity in the old grasslands are consistent with the findings of previous studies (e.g. Tilman et al. 1996; Lambers et al. 2008) which conclude that, under conditions of resource limitation, plant communities tend to be comprised of species with complementary nutrient-acquisition strategies – allowing the exploitation of a wider range of the available resources.

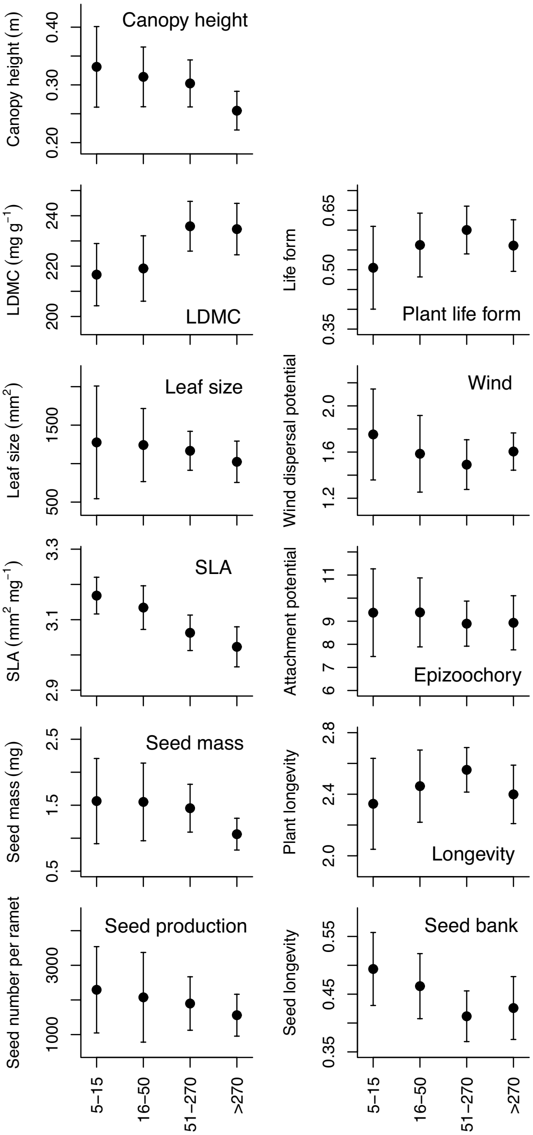

Fig. 5. Community-level mean values (mean ± 1 SD), for the eleven plant functional traits that were used to calculate functional diversity within each of the four successional age classes.

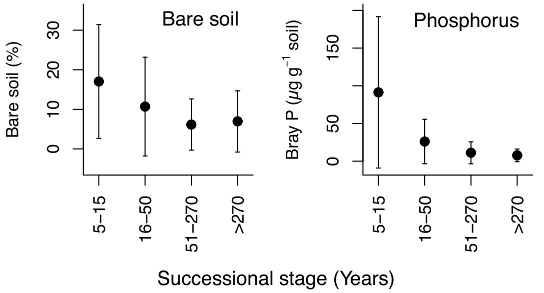

Fig. 6. Average values (± 1 SD) of the amount of bare soil (in %) and total phosphorus (per gram dry soil) within the four successional age classes.

Beta diversity

In contrast to the general increase in alpha diversity, all three aspects of beta diversity (taxonomic, functional and phylogenetic) decreased over time (Fig. 3): not only does the species composition of the communities tend to become more homogeneous, but the communities also become phylogenetically and functionally more similar during the course of succession. However, functional and phylogenetic beta diversity are both strongly positively correlated with taxonomic beta diversity which makes it difficult to assess the extent to which temporal changes in functional and phylogenetic turnover simply reflect changes in taxonomic turnover.

Null model analysis revealed that standardized effect sizes (*Beta_Stand*) of functional and phylogenetic beta diversity were positive (but never greater than 2) throughout the succession (Fig. 4): communities tended to be both functionally and phylogenetically more dissimilar than expected, given the taxonomic turnover, within all the successional stages. The temporal decline in functional similarity between time steps was steeper than expected, given the decrease in taxonomic similarity, suggesting that deterministic processes are involved in community assembly for the studied traits (cf. Fukami et al. 2005). The high *Funct_Beta_Stand* values in early and mid succession suggest that dispersal limitation and/or an underlying environmental gradient (Fig. 6) play a stronger role in determining species turnover within the early to mid successional stages than in the late successional stages (cf. Bryant et al. 2008; Swenson et al. 2011). The late successional grasslands showed considerably lower variability in phosphorus availability and the amount of bare soil than grasslands from the early and mid successional stages (Fig. 6). The tendency for communities to become increasingly functionally similar to each other as the succession proceeds is likely to reflect the fact that the environmental conditions of grasslands sites converge over time. However, lower levels of dispersal limitation in the old grasslands may also have contributed to the spatial homogenization of the communities (cf. Cadotte 2006; Purschke et al. 2011).

In contrast to the consistent decrease in functional turnover (beta diversity) with time, there was an increase in *Phyl_Beta_Stand* values between the early and the late-mid successional time steps, indicating that, although communities gradually become functionally more similar, they tend to become phylogenetically more dissimilar, given the taxonomic beta diversity, between early and mid succession. The relatively low phylogenetic turnover between communities within the early successional time step is likely to reflect the fact that early successional communities, while functionally more dissimilar than expected, may still contain closely related species that have persisted from the preceeding phase of arable cultivation.

Functional and phylogenetic diversity measures show different patterns of deviation from null expectations

There are at least two possible explanations for the fact that functional and phylogenetic (alpha and beta) diversity show different patterns of deviations from null expectations. First, phylogenetic relationships may be a poor reflection of the species' ecological similarity if the traits under consideration are not phylogenetically conserved. Blomberg's *K*-values were lower than one for all traits in our study, indicating a lack of phylogenetic signal, i.e. that closely related species are not functionally similar (Table A4 and in Supplementary material, see also Fig. A1 in Supplementary material). Second, phylogenetic diversity may represent a more inclusive overall measure of ecological similarity than measures of functional diversity, which are based on a limited set of traits (Cadotte et al. 2009; Meynard et al. 2011). However, the fact that (a) all traits in our study showed a low phylogenetic signal and (b) functional, but not phylogenetic, alpha diversity showed strong and significant deviations from random expectations, suggests that the functional traits that were used in our study are involved in the process of community assembly.

Conclusions

Comparative analysis of taxonomic, phylogenetic and functional diversity at different successional stages provides insights into the temporal dynamics of the processes that drive biodiversity changes after disturbance. Our study shows that the changes in biodiversity during arable-to-grassland succession cannot be explained by random processes, and indicates that trait-mediated environmental and dispersal filtering are likely to play a more dominant role in community assembly during early to mid succession than in the old grasslands. Short-term grazing management (<50 years), is associated with a rapid increase in species richness but does not enhance functional or phylogenetic diversity. Species entering the local communities between the early and mid successional stages are closely related and functionally redundant. In contrast, the fact that continuous grazing management over a long period of time (>270 years) promotes functional and phylogenetic diversity, without a further increase in species numbers, emphasises the high conservation value of old semi-natural grasslands. Our results suggests that biodiversity monitoring and conservation strategies should not only focus on species diversity but should also take into account the ecological and evolutionary similarity between species – both within and between communities (cf. Mayfield et al. 2010; Pavoine & Bonsall 2011; Morlon et al. 2011).

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Supplementary material

Table A1. Pearson's product-moment correlations (*r*) between eleven plant functional traits that were used to calculate functional diversity. Significant correlations are indicated by bold text.

	LDMC	Leaf size	SLA	Seed mass	Seed prod.	Plant life f.	Wind	Epizoo.	Longevity	Seed bank
Canopy height	0.13	**0.43**	0.04	**0.32**	**0.19**	0.05	-0.05	-0.13	**0.19**	-0.06
LDMC		-0.09	**-0.21**	**0.15**	**-0.22**	**0.15**	-0.07	-0.03	**0.29**	-0.11
Leaf size			0.03	**0.35**	0.1	-0.04	-0.04	**-0.19**	**0.2**	**-0.17**
SLA				-0.07	-0.08	**-0.21**	-0.08	0.11	**-0.19**	**0.19**
Seed mass					**-0.38**	0.01	**-0.56**	**-0.59**	**0.13**	**-0.46**
Seed production						-0.1	0.3	**0.27**	**-0.21**	**0.41**
Plant life form							0.07	0.04	**0.51**	**-0.19**
Wind								**0.34**	0.02	**0.21**
Epizoochory									0.03	**0.25**
Longevity										**-0.42**

Table A2. Pearson's product-moment correlations (*r*) between the taxonomic, functional and phylogenetic alpha diversity measures. Significant correlations are indicated by bold text.

	Funct_Alpha	Funct_Alpha_Stand	Phylo_Alpha	Phylo_Alpha_Stand
Species richness	**0.49**	-0.1	**0.431**	0.251
Funct_Alpha		**0.79**	**0.395**	**0.361**
Funct_Alpha_Stand			0.166	**0.274**
Phylo_Alpha				**0.927**

Table A3. Mantel correlations (*rM*) between the the taxonomic, functional and phylogenetic beta diversity measures. Significant correlations (999 permutations) are indicated by bold text.

	Funct_Beta	Funct_Beta_Stand	Phyl_Beta	Phyl_Beta_Stand
Tax_Beta	**0.981**	**0.166**	**0.858**	-0.04
Funct_Beta		**0.335**	**0.867**	0.007
Funct_Beta_Stand			**0.262**	**0.291**
Phyl_Beta				**0.442**

Table A4. The phylogenetic signal (Blomberg's *K*) in each of the eleven functional traits. *K* values of less than 1 indicate a weak phylogenetic signal.

Trait	*K*
Canopy height	0.14
LDMC	0.329
Leaf size	0.209
SLA	0.164
Seed mass	0.293
Seed production	0.147
Plant life form	0.222
Wind	0.22
Epizoochory	0.169
Longevity	0.189
Seed bank	0.19

Fig. A1. Distribution of the eleven plant functional traits across the phylogeny of the 234 plant species. Trait values were standardized to mean = 0 and SD = 1.

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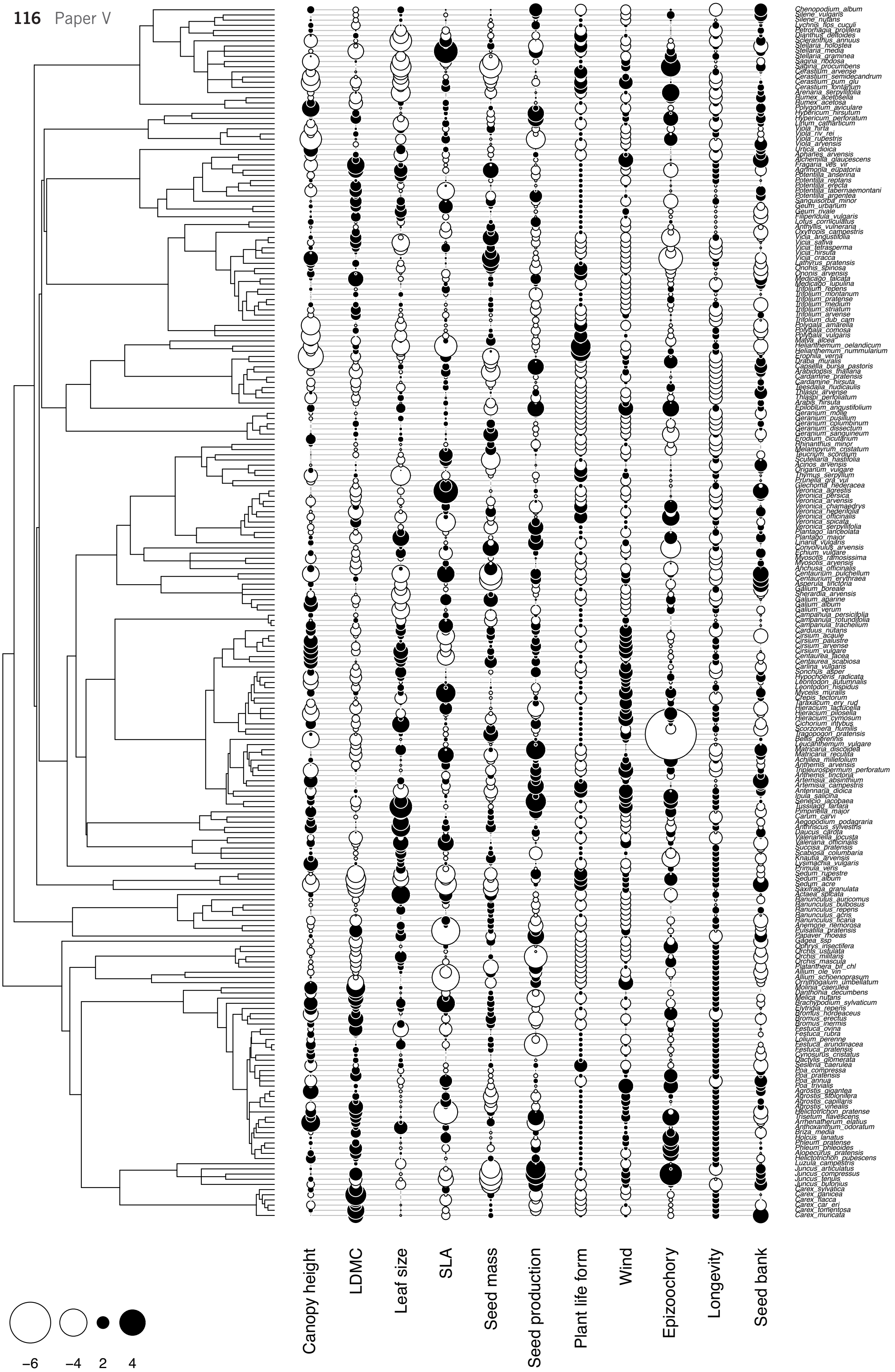
Chenopodium_album
Silene_vulgaris
Silene_nutans
Lychnis_flos_cuculi
Petrorhagia_prolifera
Dianthus_deltoides
Scleranthus_annuus
Stellaria_holostea
Stellaria_media
Stellaria_graminea
Sagina_nodosa
Sagina_procumbens
Cerastium_arvense
Cerastium_semidecandrum
Cerastium_pum_glu
Cerastium_fontanum
Arenaria_serpyllifolia
Rumex_acetosella
Rumex_acetosa
Polygonum_aviculare
Hypericum_hirsutum
Hypericum_perforatum
Linum_catharticum
Viola_hirta
Viola_riv_rei
Viola_rupestris
Viola_arvensis
Urtica_dioica
Aphanes_arvensis
Alchemilla_glaucescens
Fragaria_ves_vir
Agrimonia_eupatoria
Potentilla_anserina
Potentilla_reptans
Potentilla_erecta
Potentilla_tabernaemontani
Potentilla_argentea
Sanguisorba_minor
Geum_urbanum
Geum_rivale
Filipendula_vulgaris
Lotus_corniculatus
Anthyllis_vulneraria
Oxytropis_campestris
Vicia_angustifolia
Vicia_sativa
Vicia_tetrasperma
Vicia_hirsuta
Vicia_cracca
Lathyrus_pratensis
Ononis_spinosa
Ononis_arvensis
Medicago_falcata
Medicago_lupulina
Trifolium_repens
Trifolium_montanum
Trifolium_pratense
Trifolium_medium
Trifolium_striatum
Trifolium_arvense
Trifolium_dub_cam
Polygala_amarella
Polygala_comosa
Polygala_vulgaris
Malva_alcea
Helianthemum_oelandicum
Helianthemum_nummularium
Erophila_verna
Draba_muralis
Capsella_bursa_pastoris
Arabidopsis_thaliana
Cardamine_pratensis
Cardamine_hirsuta
Teesdalia_nudicaulis
Thlaspi_arvense
Thlaspi_perfoliatum
Arabis_hirsuta
Epilobium_angustifolium
Geranium_molle
Geranium_pusillum
Geranium_columbinum
Geranium_dissectum
Geranium_sanguineum
Erodium_cicutarium
Rhinanthus_minor
Melampyrum_cristatum
Teucrium_scordium
Scutellaria_hastifolia
Acinos_arvensis
Origanum_vulgare
Thymus_serpyllum
Prunella_gra_vul
Glechoma_hederacea
Veronica_agrestis
Veronica_persica
Veronica_arvensis
Veronica_chamaedrys
Veronica_hederifolia
Veronica_officinalis
Veronica_spicata
Veronica_serpyllifolia
Plantago_lanceolata
Plantago_major
Linaria_vulgaris
Convolvulus_arvensis
Echium_vulgare
Myosotis_ramosissima
Myosotis_arvensis
Anchusa_officinalis
Centaurium_pulchellum
Centaurium_erythraea
Asperula_tinctoria
Galium_boreale
Sherardia_arvensis
Galium_aparine
Galium_album
Galium_verum
Campanula_persicifolia
Campanula_rotundifolia
Campanula_trachelium
Carduus_nutans
Cirsium_acaule
Cirsium_palustre
Cirsium_arvense
Cirsium_vulgare
Centaurea_jacea
Centaurea_scabiosa
Carlina_vulgaris
Sonchus_asper
Hypochoeris_radicata
Leontodon_autumnalis
Leontodon_hispidus
Mycelis_muralis
Crepis_tectorum
Taraxacum_ery_rud
Hieracium_lactucella
Hieracium_pilosella
Hieracium_cymosum
Cichorium_intybus
Scorzonera_humilis
Tragopogon_pratensis
Bellis_perennis
Leucanthemum_vulgare
Matricaria_discoidea
Matricaria_recutita
Achillea_millefolium
Anthemis_arvensis
Tripleurospermum_perforatum
Anthemis_tinctoria
Artemisia_absinthium
Artemisia_campestris
Antennaria_dioica
Inula_salicina
Senecio_jacobaea
Tussilago_farfara
Pimpinella_major
Carum_carvi
Aegopodium_podagraria
Anthriscus_sylvestris
Daucus_carota
Valerianella_locusta
Valeriana_officinalis
Succisa_pratensis
Scabiosa_columbaria
Knautia_arvensis
Lysimachia_vulgaris
Primula_veris
Sedum_rupestre
Sedum_album
Sedum_acre
Saxifraga_granulata
Actaea_spicata
Ranunculus_auricomus
Ranunculus_bulbosus
Ranunculus_repens
Ranunculus_acris
Ranunculus_ficaria
Anemone_nemorosa
Pulsatilla_pratensis
Papaver_rhoeas
Gagea_ssp
Ophrys_insectifera
Orchis_ustulata
Orchis_militaris
Orchis_mascula
Platanthera_bif_chl
Allium_ole_vin
Allium_schoenoprasum
Ornithogalum_umbellatum
Molinia_caerulea
Danthonia_decumbens
Melica_nutans
Brachypodium_sylvaticum
Elytrigia_repens
Bromus_hordeaceus
Bromus_erectus
Bromus_inermis
Festuca_ovina
Festuca_rubra
Lolium_perenne
Festuca_arundinacea
Festuca_pratensis
Cynosurus_cristatus
Dactylis_glomerata
Sesleria_caerulea
Poa_compressa
Poa_pratensis
Poa_annua
Poa_trivialis
Agrostis_gigantea
Agrostis_stolonifera
Agrostis_capillaris
Agrostis_vinealis
Helictotrichon_pratense
Trisetum_flavescens
Arrhenatherum_elatius
Anthoxanthum_odoratum
Briza_media
Holcus_lanatus
Phleum_pratense
Phleum_phleoides
Alopecurus_pratensis
Helictotrichon_pubescens
Luzula_campestris
Juncus_articulatus
Juncus_compressus
Juncus_tenuis
Juncus_bufonius
Carex_sylvatica
Carex_panicea
Carex_flacca
Carex_car_eri
Carex_tomentosa
Carex_muricata
Canopy height
LDMC
Leaf size
SLA
Seed mass
Seed production
Plant life form
Wind
Epizoochory
Longevity
Seed bank
−6
−4
2
4

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