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Citation for published version (APA):

Purschke, O. (2011). *Plant community assembly and biodiversity: a spatio-temporal perspective*. [Doctoral Thesis (monograph), Dept of Physical Geography and Ecosystem Science]. Department of Earth and Ecosystem Sciences, Lund University.

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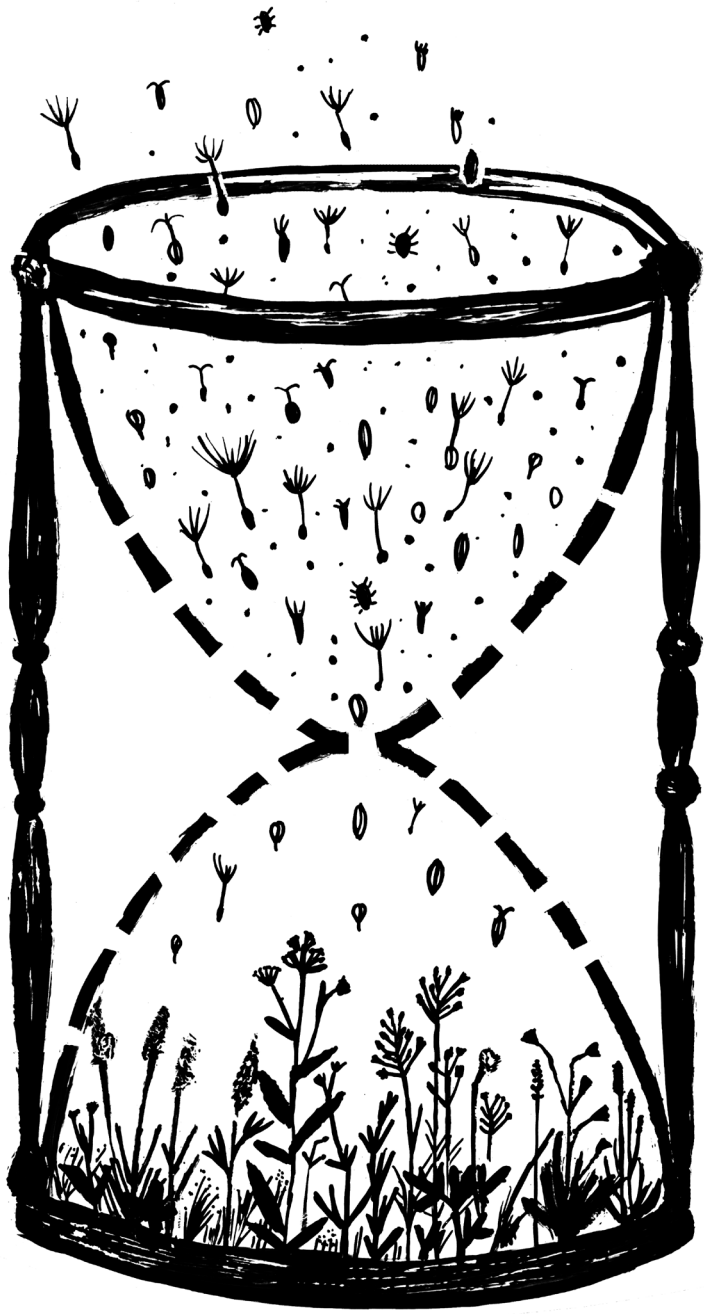
Plant community assembly & biodiversity

A spatio-temporal perspective

Oliver Purschke

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Lund University, 2011





Organization LUND UNIVERSITY Department of Earth and Ecosystem Sciences Sölvegatan 12 SE-22362 Lund, Sweden		Document name DOCTORAL DISSERTATION	
		Date of issue December 2nd, 2011	
		Sponsoring organization	
Author(s) Oliver Purschke			
Title and subtitle Plant community assembly and biodiversity: a spatio-temporal perspective			
Abstract <p>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.</p>			
Key words: dispersal, functional diversity, landscape fragmentation, land use history, life-history traits, null model, phylogenetic diversity, semi-natural grasslands			
Classification system and/or index terms (if any):			
Supplementary bibliographical information: Meddelanden från Lund universitetets geografiska institution. Avhandling 195		Language English	
ISSN and key title: 0346-6787		ISBN 978-91-85793-21-1	
Recipient's notes		Number of pages 124	Price
		Security classification	

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Meddelanden från Lunds universitets geografiska institution.
Avhandling 195

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Graphic design and illustration: Friederike Arndt (www.formenorm.de)
Printed at Tryckeriet i E-huset, Lund, Sweden, 2011

ISSN: 0346-6787

ISBN: 978-91-85793-21-1

Academic Dissertation

for the degree of Doctor of Philosophy at the Faculty of Science, to be publicly defended on December 2nd 2011 at 10.00 a.m. in room Världen, Geocentrum I, Sölvegatan 10, Lund.

The thesis will be defended in English.

Faculty opponent: Professor James M. Bullock, Centre for Ecology and Hydrology, Wallingford, Oxfordshire, UK

Lund 2011

Plant community assembly & biodiversity

A spatio-temporal perspective

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Lund University, Lund 2011

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.

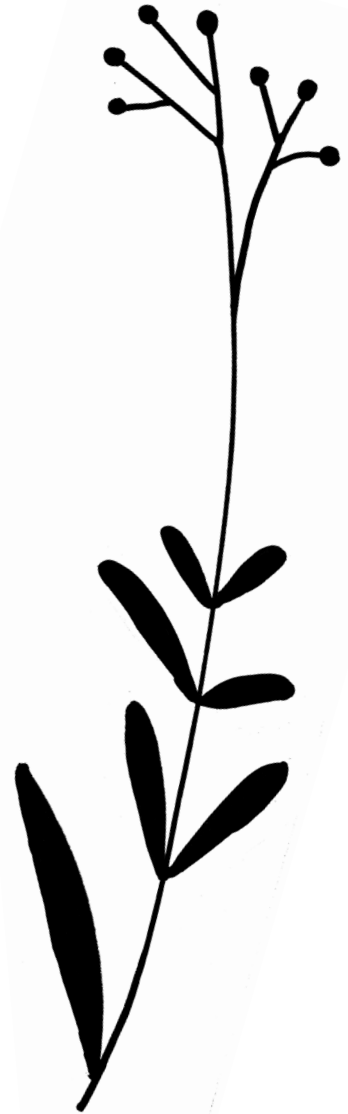
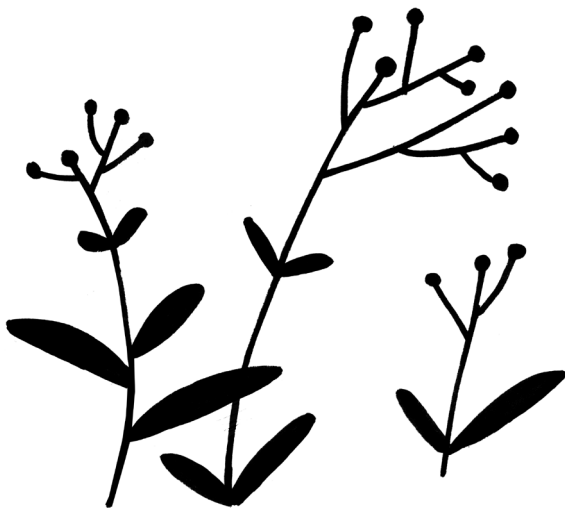
Paper V: I compiled/derived trait data from data bases, analysed the data and had the main responsibility for the writing of the paper.

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Plant community assembly & biodiversity

A spatio-temporal perspective



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 dis-

persal 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 there-

fore 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 function-

al 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 re-

stricted 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 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-

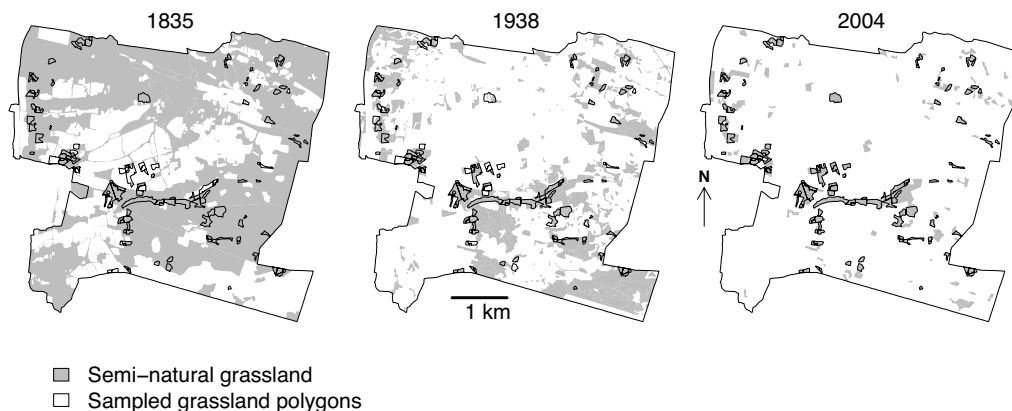


Fig. 1. Land-cover maps of the Jordtorp study area for three time periods (1835, 1938 and 2004). The 113 grassland polygons in which vegetation for the studies in Papers I–III was sampled are indicated.

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 Sørensen's index. For phylogenetic and functional beta diversity, the Sørensen 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 di-

versity 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 inves-

tigated 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 & Poschold 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 be 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 depend-

ent 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.

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.

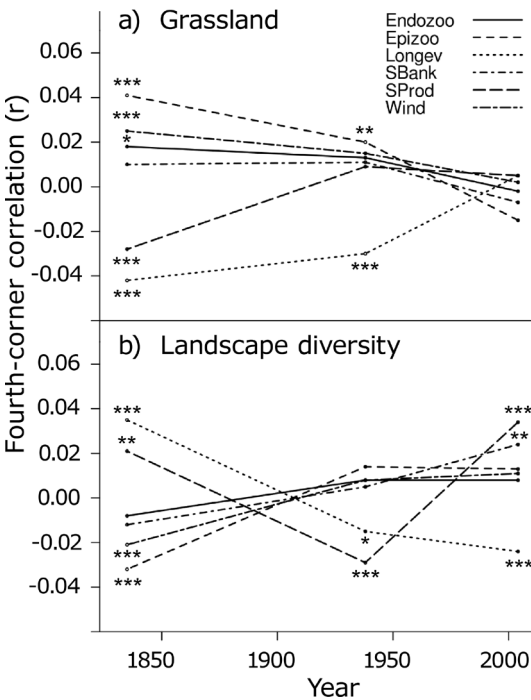


Fig. 2. Correlations between the six dispersal traits and a) percentage of grassland and b) diversity of the surrounding landscape at three time intervals: present-day (2004) and past (1835 & 1938). Significant relationships are indicated *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$.

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

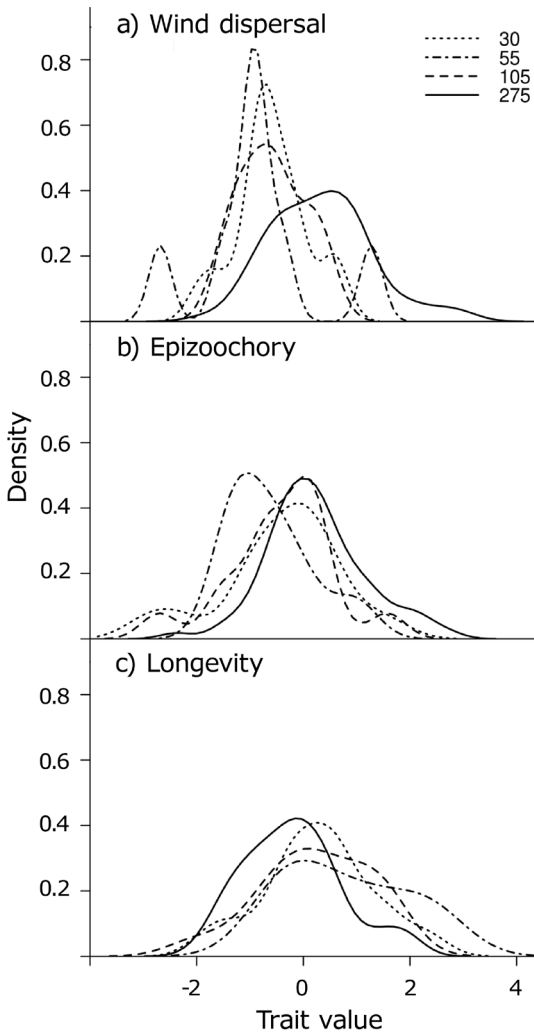


Fig. 3. Probability density plots showing the distribution of a) wind dispersal potential, b) epizoochory and c) adult plant longevity for different grassland age classes (30, 50, 105 and 275 years of grazing continuity). Mean trait values (at the grassland polygon level) were standardized with mean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

pected 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

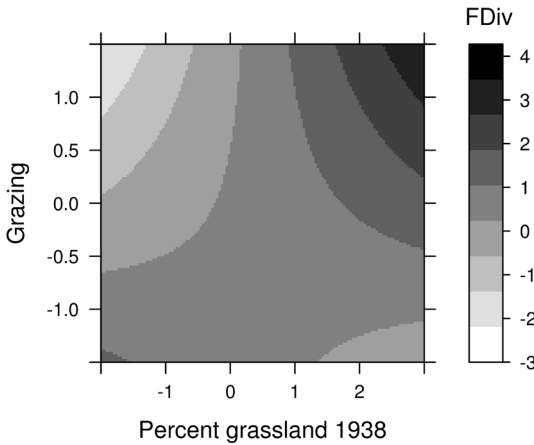


Fig. 4. Dispersal trait diversity (FDiv; light grey to black shading) in response to the interaction between present-day grazing intensity (Grazing) and amount of grassland in the historical landscape in 1938.

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,

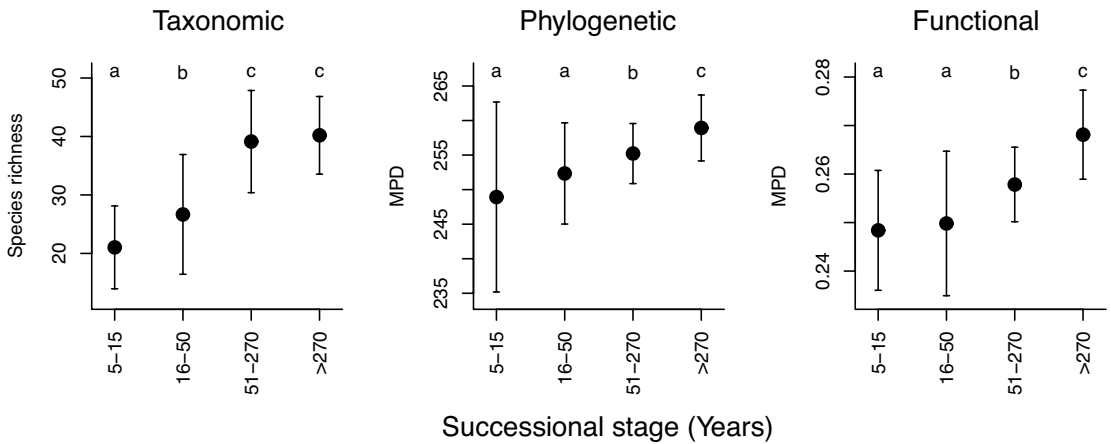


Fig. 5. Taxonomic, phylogenetic and functional alpha diversity (mean \pm 1 SD) within four successional age classes. Phylogenetic and functional alpha diversity are represented by the mean pairwise distance (MPD). Letters indicate significant differences between the successional timesteps.

which favours species that have a high long-dispersal potential. We also found that early and early-mid successional communities mainly con-

sisted 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).

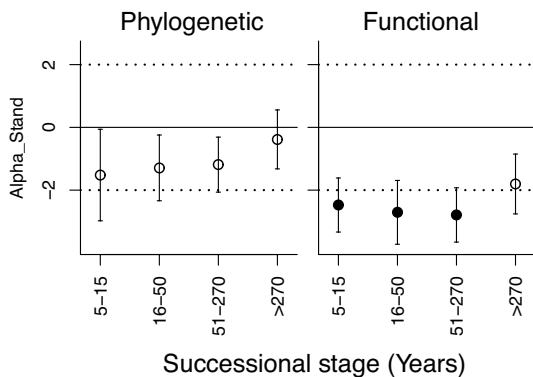


Fig. 6. Standardized effect sizes of phylogenetic and functional alpha diversity (mean \pm 1 SD). Values $<$ 0 indicate that phylogenetic or functional alpha diversity is lower than expected, given the species richness. The dotted lines indicate the 0.05 significance levels. Values $<$ -2 (black dots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

persal 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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Acknowledgements

First and foremost I would like to thank my supervisors Martin, Honor and Peter for accepting me for this position, and for the guidance and support throughout my Ph.D. project. I learned a lot from working with you:

Martin, you taught me to think more straight and to always keep the bigger picture in mind. Although your schedule was usually packed you always made time for personal meetings, and responded to emails within a few minutes (sometimes even after 10 p.m.!). Anyway, I am glad you were wrong when you said that doing my Ph.D. will not always be fun.

Honor, it has been a great pleasure to work with you. Your passion for science, but also for many real life things, is extremely motivating and driving. You were also a great writing teacher to me.

Peter, thanks for hosting me in Regensburg at the beginning of my project, and for always making time for long in-depth discussions. You are full of ideas and it is great that you share them with others. Your enthusiasm is really infectious. Still looking forward to have a table tennis match with you.

I would like to thank the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS) and Lund University for financial support. Having a Ph.D. education in Sweden, with all the great courses and excursions, was a privilege for me.

I want to thank my collaborators Ingolf, Marten, Stefan and Walter for intense and fruitful discussions at the Department of Community Ecology at the UFZ in Halle.

Thanks to Christine Römermann for sharing trait data and to Oliver Tackenberg for letting me work in his lab in Frankfurt/Main in spring 2008. I also thank Eje Rosén and the staff at Station Linné on Öland where I carried out my field work.

I would also like to thank the Jordtorp group: Honor, Martin, Karin, Triin, Marie, Lotten, Barbara, Thomas and Jonas. Hope we can collaborate further in the future. Barbara, thanks for collecting and sharing the succession data set, and thanks to Marie for hosting me when I first arrived in Lund.

Thanks to all my colleagues at ENES, I very much enjoyed the working atmosphere during the time I was sitting there. Torben, Sardu, Elin and Julia B., thanks for the great weekend trips, concerts and movie evenings.

I would also like to thank my Ph.D. colleagues at the Biodiversity unit in the Ecology building for the relaxed fikas: Anja, Anneli, Frida, Johanna, Therese, Yuan, Barbara, Linda-Maria, Eman, Tim, Georg, Josef and Erkki. Pål-Axel, Stefan and Micke for discussions during lunch breaks. Josefin, thanks for your kindness and for all your help with practical things, especially at the end of my thesis.

Alwyn and Erkki, I very much enjoyed to hang out with you after work. Alwyn, it has been great to meet you during my last months here and I am looking forward to some joint hiking in the future. Torben, Julia G., Sardu and Johan, thanks for letting me feel home in Lund. Torben, I always enjoyed discussing R-stuff with you, especially at the weekends.

I would also like to thank Carsten Dormann for introducing me to the world of number crunching in R when I was an undergrad. Klaus Birkhofer, thanks for very emotional discussions about multivariate stats. Joe, Ben, Veiko and the people at the LUNARC - Centre for Scientific and Technical Computing, thanks for providing access to computational resources.

Thanks to the people at Kansliet in ENES, Eva and Galina for their invaluable help with administrative issues.

Honor C. Prentice and Alwyn Williams kindly improved the English in the summary of this thesis and Triin Retailu provided Figure 1.

I would like to thank my family for their support and for always believing in what I am doing. Hopefully we meet a bit more often in the future.

Finally, I would like to thank you, Frieda, the most important person to me (+ thanks for the layout of my thesis).

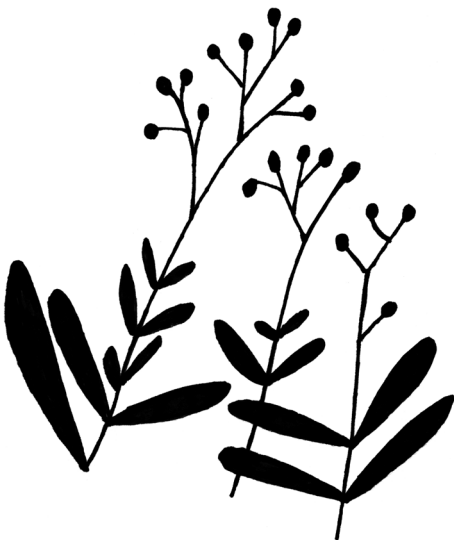
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ISBN: 978-91-85793-21-1
Tryckeriet i E-huset, Lund, 2011